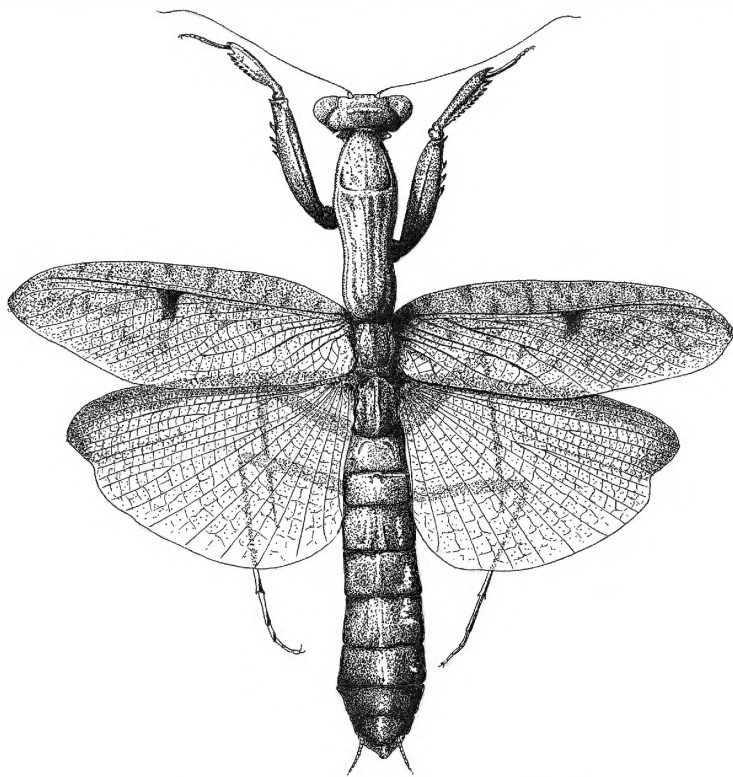


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AUSTRALIAN SPECIES OF *DICRANOMYIA* (*IDIOGLOCHINA*) (DIPTERA: TIPULOIDEA: LIMONIIDAE)

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Abstract

The species of *Dicranomyia* (*Idioglochina*) Alexander, 1921 known from Australia are reviewed in detail and a new species, *Dicranomyia* (*Idioglochina*) *caloundrae* sp. n. is described. This new species from the littoral zone of a marine rocky shore at Caloundra, Queensland, is illustrated and compared with the two species previously known from Australia, and a key to the males of Australian *Dicranomyia* (*Idioglochina*) is presented. Observations on the biology of the new species as made by the collector (AGO) and life photographs are presented.

Key Words: marine insects, natural history, new species

Introduction

The species of the *Dicranomyia* Stephens, 1829 subgenus *Idioglochina* Alexander, 1921 may be restricted to at least some of the lands surrounded by or bordering the Pacific and Indian oceans (known from Australia, New Guinea, Indonesia, Taiwan, Japan, New Zealand, New Caledonia, Vanuatu, Tonga, Samoa, Micronesia, Mauritius, Comoros, Seychelles, South Africa, Canada, USA, Chile). From the known habits and general occurrence it appears that all species are marine or coastal and require saltwater as a habitat for the early stages (Alexander 1972). In the World Catalogue of Tipuloidea 28 species-group taxa are listed, among them two species from tropical Australia (Oosterbroek 2019). The collection by the third author of a *D. (Idioglochina)* species from subtropical Australia was therefore sufficient reason to review the information and material available on the described Australian species (Fig. 1). The state of the type specimens created problems and made it necessary for us to repeat the complete original descriptions of both species. The fresh material from Caloundra is described as new below. Also described and illustrated are larva and pupal exuviae. Biological observations, including a quantitative study of phenology, are provided.

Materials and Methods

Specimens of adults were collected by AGO either by hand or using an aerial insect net and preserved dry or in 70% ethanol; immature stages were recovered from scrapings of *Corallina* algae examined under a dissecting microscope; pupal exuviae were removed from the algal substrate by hand when they could be located by the presence of an emerging adult. Immature stages were preserved in 70% ethanol. As a result of this preservation, the coloration of specimens might have changed from the natural state. The illustrations of the male genitalia

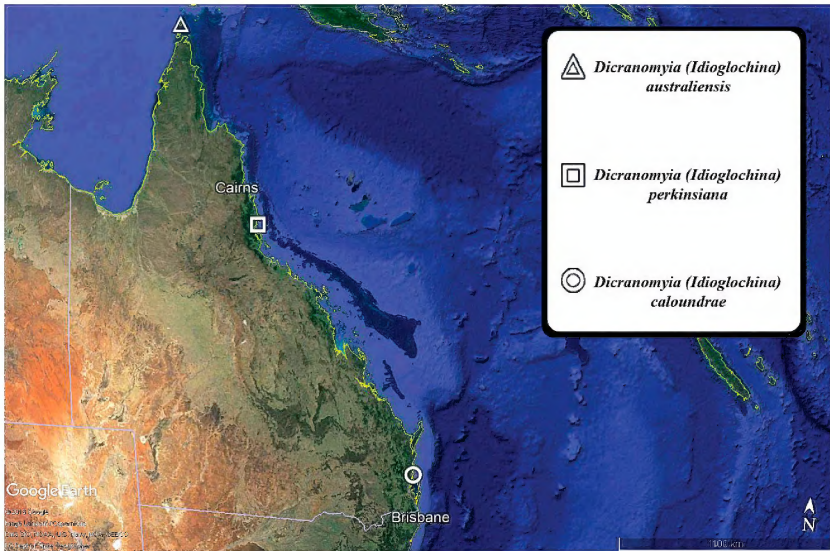


Fig. 1. Distribution of the Australian species of *Dicranomyia* (*Idioglochina*), image modified from SIO, NOAA, U.S. Navy, NGA, GEBCO map data, Google Earth.

(hypopygium) are from specimens cleared in KOH and displayed in glycerol.

Type material of known species deposited in the Alexander Collection (AC) in the Smithsonian Institution (SI) in Washington DC and in the Queensland Museum (QM) was studied. Specimens of the newly described species have been lodged in the Queensland Museum (QM) in Brisbane, the Australian Museum (AM) in Sydney, in the AC (Alexander Collection, Smithsonian Institution, in Washington D.C.) and in the Museum Victoria (NMV) in Melbourne. Specimens retained by the second author are kept in a vouchered research collection at the GHD Water Sciences Laboratory in Melbourne to aid in ongoing survey work and for use in DNA barcoding studies. DNA sequencing efforts are ongoing; sequence and specimen data are stored in the Barcode of Life Data Systems (BOLD) database and, upon any future publication of genetic data, sequences will be published to GenBank.

Descriptive terminology for the new species is in accord with McAlpine (1981). In the descriptive texts taken from Alexander (1922, 1930) his original terms are preserved.

Casual observations of phenology were made by AGO during 2017 and 2018, chiefly at low spring tides in the afternoons from June to September. From 26 June to 6 August 2019 inclusive a quantitative estimate of relative abundance was made each day at approximately low tide. A transect of 40 m was walked at a steady pace with individuals 1 m either side counted. On these days a sample of

10–20 specimens were collected and released to monitor the sex ratio, and various behavioural observations were recorded.

Systematics

Genus *Dicranomyia* Stephens

Dicranomyia Stephens, 1829: 32.

Type species: *Limnobia modesta* Meigen, 1818, by designation of Coquillett, 1910: 533.

Subgenus *Idioglochina* Alexander

Dicranomyia (*Idioglochina*) Alexander, 1921: 207.

Limonia (*Idioglochina*) Alexander, 1928: 241.

Type species: *Rhipidia tusilata* Alexander, 1921, by original designation.

Diagnosis (from Theischinger 1996). Mouth-parts shorter than remainder of head; antenna 14-segmented, flagellomeres markedly extended to produce serrate to almost pectinate appearance (particularly in male); eyes glabrous; wing venation: Sc short, ending well proximal to origin of Rs; three branches of R reaching margin; M with two branches; dm not hexagonal or proximally pointed; r-m not in direct alignment with Rs; CuA2 not fused with A1; no supernumerary crossveins.

Dicranomyia (*Idioglochina*) *australiensis* Alexander

(Figs 1–6)

Dicranomyia (*Idioglochina*) *australiensis* Alexander, 1922: 581.

Holotype ♂. North Australia, Moa Isl., 1921, G.F. Hill. Studied, photographs figs 2–6.

According to Alexander (1922) the holotype was preserved in the collection of the writer. In 1989 GT did not find it in AC (SI). In 2019, however it was found in QM, having been sent in 1983 on loan to E.N. Marks (1918–2002) (J. Gelhaus pers. comm.). Marks, who had an interest in marine fly fauna, retired in 1983 following 10 years working at the Queensland Institute of Medical Research (QIMR), Brisbane. Her collection, mainly of mosquitoes, was transferred from QIMR to the University of Queensland shortly after. The University of Queensland Insect Collection was donated to the Queensland Museum in 2011 (G. Daniels & C. Lambkin (QM) pers. comm.)

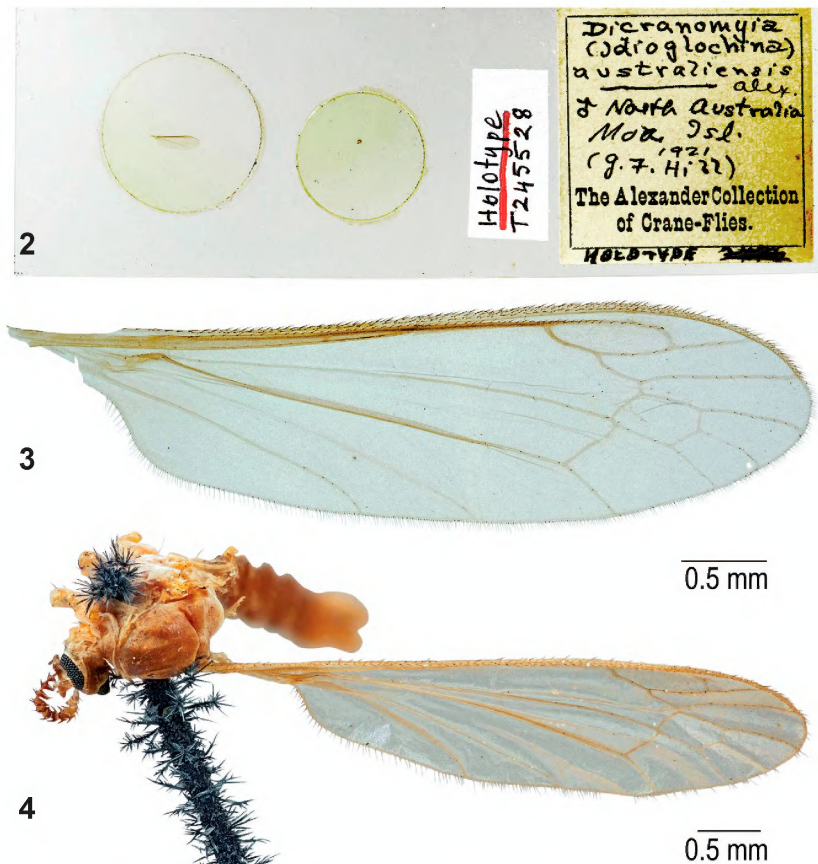
Description (from Alexander 1922).

General colouration brown, the pleura pruinose; wings grey; cell 1st M2 about as long as vein Cu1 beyond it.

♂. Length, 4.5 mm; wing, 4.8 mm. ♀. Length, 4.5 mm; wing, 5 mm.

Rostrum and the very short palpi brown. Antennae light yellowish-brown, the scape a little more yellowish. Head brown, the orbits somewhat paler.

Mesonotum greyish brown, the dorsum clearer brown, the humeral region



Figs 2–4. *Dicranomyia* (*Idioglochina*) *australiensis* Alexander, holotype ♂: (2) slide with antenna, wing and label; (3) wing; (4) part of specimen.

slightly paler; scutellum obscure yellow. In the female, the mesonotum is more rufous brown. Pleura grey, the lateral sclerites of the postnotum more whitish. Halteres yellow, the knobs brown. Legs with the coxae brown, dusted with grey; trochanters yellowish-brown; remainder of the legs pale brown. Wings grey; veins brown. Venation: As in *D. (I.) debeauforti* (de Meijere) but Rs more gently arcuated, so cell 1st R1 is elongate-oval in outline; cell 1st M2 about as long as vein Cu1 beyond it. In the female, Rs is straighter.

Abdomen brown, the hypopygium obscure yellow. Ovipositor with the valves long and straight.

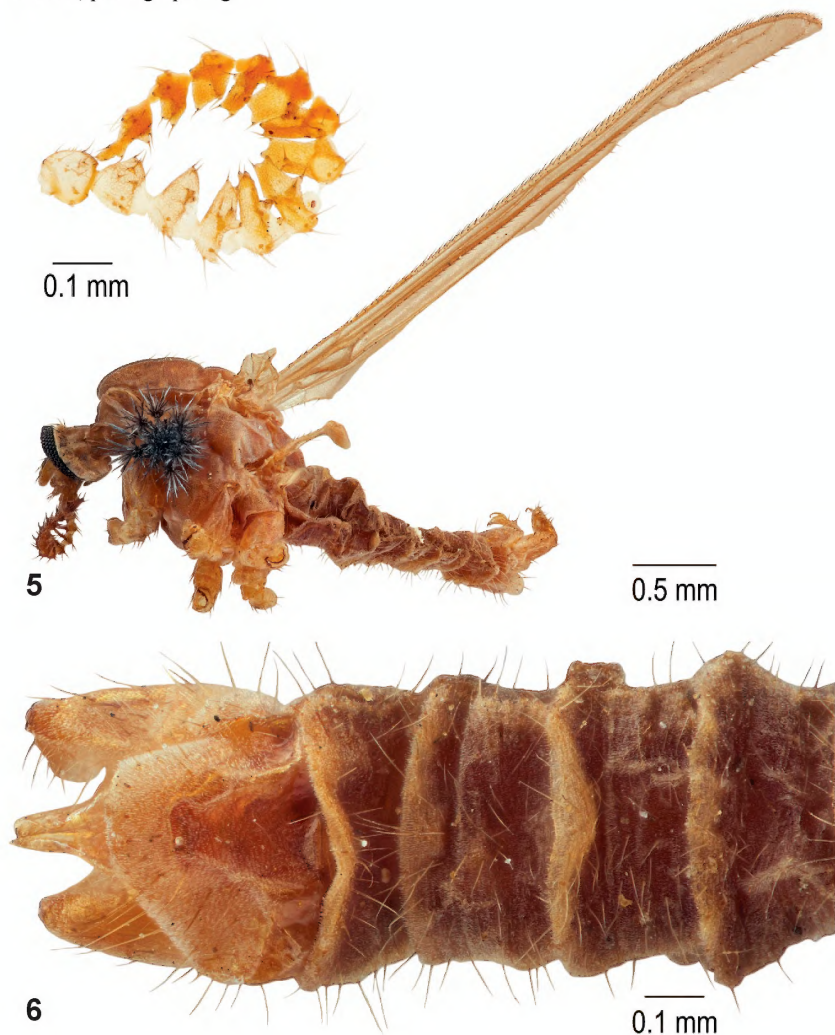
Distribution. Known from the type locality only.

***Dicranomyia (Idioglochina) perkinsiana* (Alexander)**
(Figs 1, 7–10)

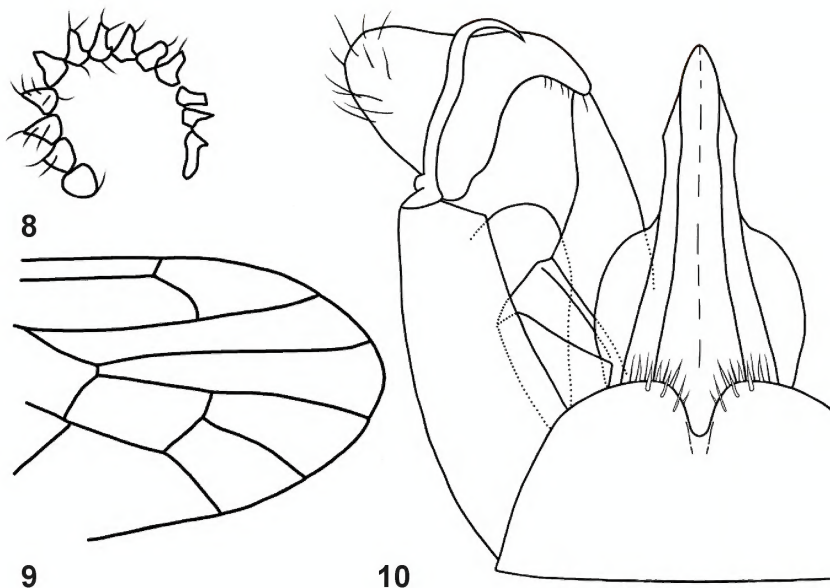
Limonia (Idioglochina) perkinsiana Alexander, 1930:154.

Holotype ♂. Queensland, Dunk Is., August 25, 1927, F.A. Perkins, QM (T245529).

Studied, photograph Fig. 7.



Figs 5, 6. *Dicranomyia (Idioglochina) australiensis* Alexander, holotype ♂: (5) part of specimen with detail of antenna; (6) abdomen, ventral.



Figs 7–10. *Dicranomyia (Idioglochina) perkinsiana* Alexander, holotype ♂: (7) specimen with labels (QM) and box (AC); (8–10) sketches from holotype slide 1989: (8) antenna; (9) wing tip; (10) part of male terminalia, dorsal.

According to Alexander (1930) the holotype is preserved in the collection of the University of Queensland which is now in the Queensland Museum. In 1989, however, GT found a slide with antenna, wing and terminalia in AC (SI). In 2019 the holotype was found in QM (Fig. 7) with indications in the AC (Fig. 7) it may have been sent in 1983 from the Smithsonian to E.N. Marks (1918–2002) (J. Gelhaus pers. comm.). Also in 2019 the slide with antenna, wing and terminalia was not found in AC (J. Gelhaus pers. comm.). Fortunately, GT had made in 1989 a sketch of what he found significant on the holotype slide (Figs 8–10). This now may well be all we have left of the holotype slide.

Description (from Alexander 1930).

Male. Length about 6 mm; wing 7.5 mm.

Rostrum dark brown, nearly as long as the remainder of the head; palpi dark brown. Antennae dark brown, the first segment more pruinose; flagellar segments strongly produced beneath, as in the *tusitala* group, the apical necks short and stout. Head pale reddish brown, sparsely pruinose, the median region of the vertex more infuscated.

Mesonotal praescutum with the interspaces brown, the disk with four dark brown stripes, the lateral and posterior portions of the sclerite dark greyish plumbeous; pseudosutural foveae punctiform, dark brown; scutum light grey medially, each lobe with two dark brown areas; scutellum and postnotum light grey. Pleura dark brownish grey, the dorso-pleural membrane buffy. Halteres obscure yellow. Legs with the coxae dark brown, pruinose, the apices restrictedly pale; remainder of legs dark brown, the femoral bases only a trifle brighter; claws with a series of about four teeth, the outermost longest. Wings with a strong dusky tinge, Rs and Cu more suffused with still darker brown; veins yellowish brown, some darker brown. Venation: Sc relatively long, the distance on costa between Sc1 and origin of Rs about two-thirds the length of the latter; basal section of R4+5 about two-thirds Rs; R2+3 only gently arcuated; m-cu shortly beyond the fork of M.

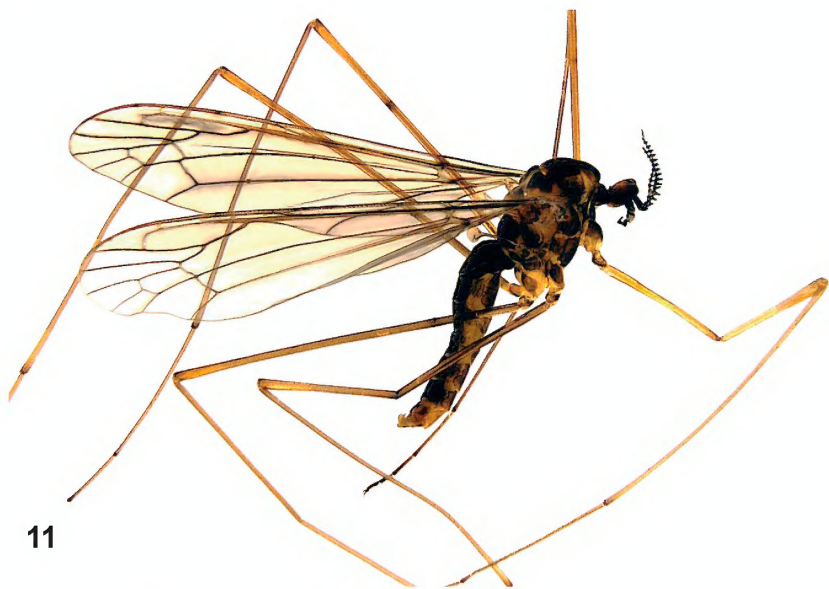
Abdominal segments dark brown, the tergites vaguely more reddish brown medially at base; caudal margins of the segments very restrictedly pale; sternites obscure brownish yellow, darker laterally, the caudal margins narrowly pale; hypopygium more brightened. Male hypopygium with the caudal margin of the ninth tergite with a small but deep V-shaped median notch. Dorsal dististyle strongly curved, sickle-shaped, narrowed to the subacute apex. Ventral dististyle with the inner beak-like portion stout, the tip obtuse.

Distribution. Known from the type locality only.

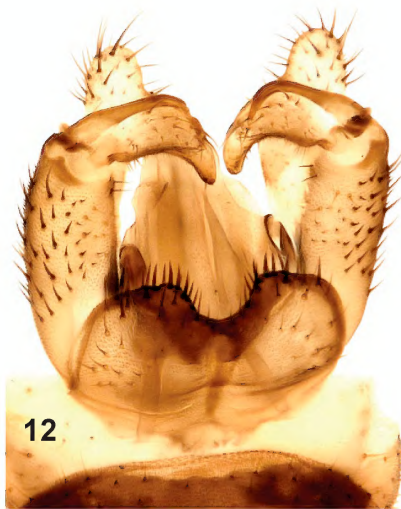
***Dicranomyia (Idioglochina) caloundrae* sp. n.**
(Figs 1, 11–29)

Material Examined. *Holotype* ♂, Australia, Queensland, Kings Beach, Caloundra, 26°48'12"S 153°08'48"E, 15-vi-2019, leg. A.G. Orr, QM (T246557).

Paratypes, same data as holotype: 3 ♂, 2 ♀, QM (T246558–T246562); 3 ♂, 2 ♀,



11



12



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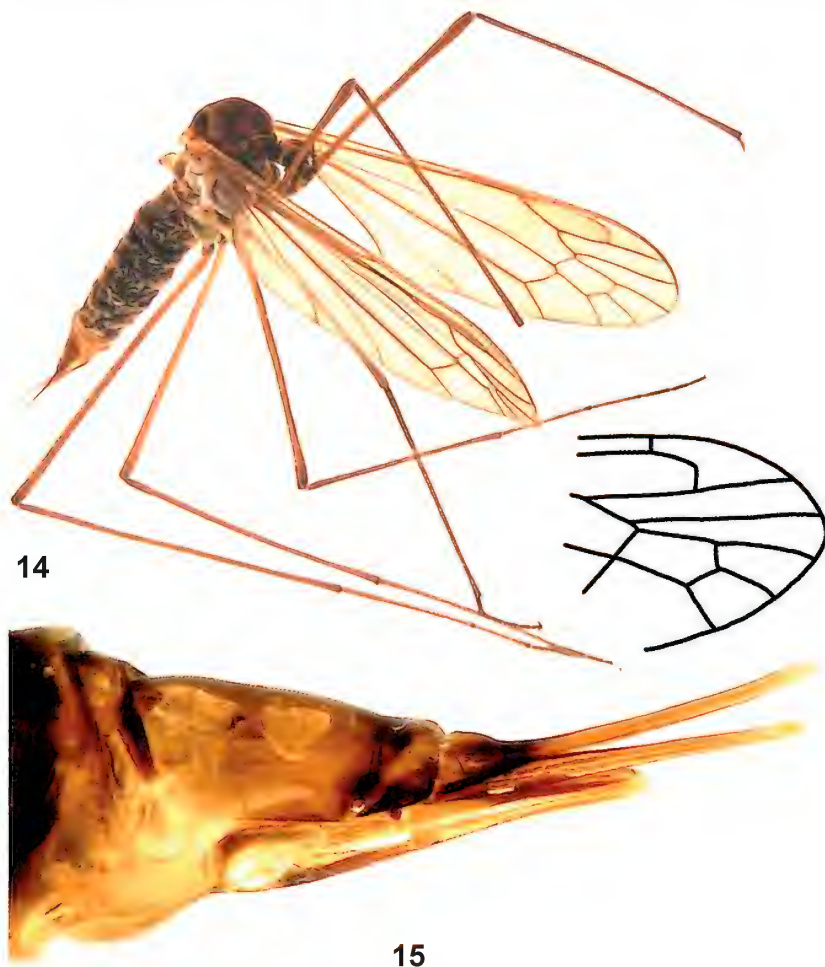
Figs 11–13. *Dicranomyia (Idioglochina) caloundrae* sp. n.: (11) ♂ habitus; (12–13) male terminalia: (12) dorsal; (13) ventral.

AM (K.393382–K.393386); 1 ♂, 1 ♀, ANIC (29-062219, 29-062220); 2 ♂, AC (USNMENT01519731–USNMENT01519732) ; 3 ♂, 1 ♀, NMV (T-22489–T-22492); 2 ♂, 1 ♀, GHD (T24683– T24684).

Larvae: 4, GHD (TL1697–TL1700).

Pupae: 11 exuviae, GHD.

Description. Male (Figs 11–13). Body length (excluding antenna) 7.4 mm, wing



Figs 14, 15. *Dicranomyia (Idioglochina) caloundrae* sp. n.: (14) ♀ habitus with insert wingtip; (15) female terminalia, lateral.



Fig. 16. *Dicranomyia (Idioglochina) caloundrae* sp. n., larvae, habitus.

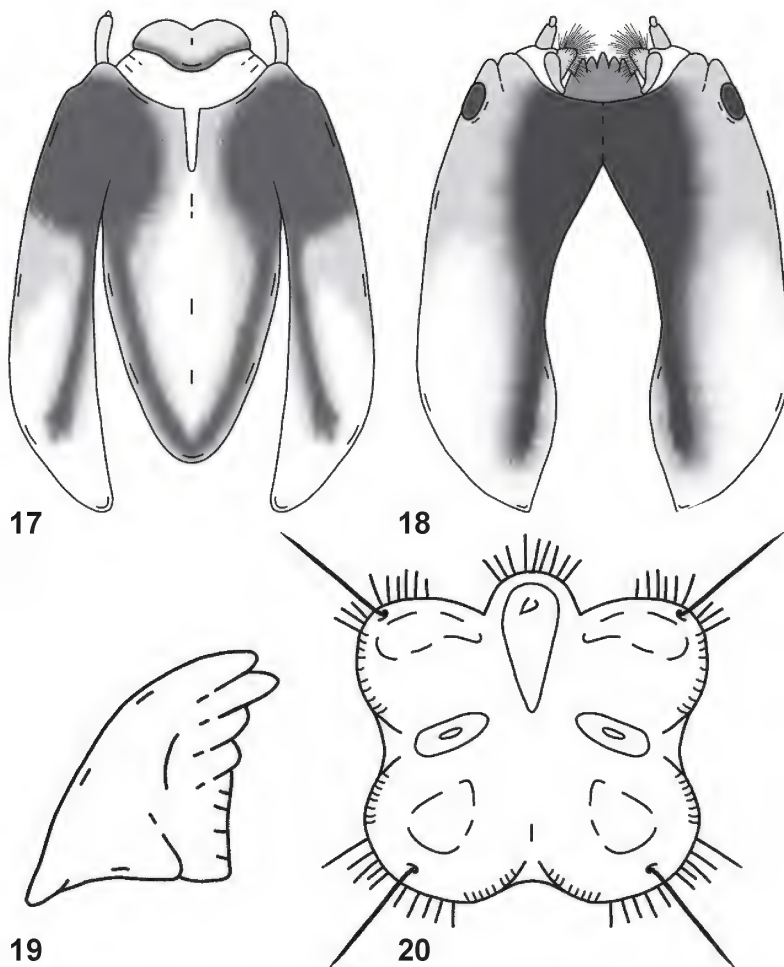
length 9.7 mm.

Head brown, vertex darker greyish brown, antennal scape and pedicel brown, flagellomeres yellowish brown, palpus dark brown. Flagellomeres ventrally produced, subpectinate, extensions on flagellomeres 4–10 more prominent than on basal or terminal segments. Antenna extending back to prescutal suture.

Pronotum greyish brown. Prescutum, scutum, mediotergite and scutellum greyish brown, paler golden brown at prescutal pit, centre of transverse suture and lateral angles of scutal lobes. Pleura pale greyish brown. Coxae greyish brown, trochanters yellowish brown, femora, tibiae and tarsi greyish brown.

Wing hyaline, veins greyish brown. Distance on costa between Sc1 and origin of Rs slightly greater than two-thirds length of Rs; basal section of R4+5 one-half length of Rs; R2 strongly arcuated to bend at angle (as in Fig. 14); m-cu very slightly proximal to fork of M. Halter with stem yellowish brown and knob whitish.

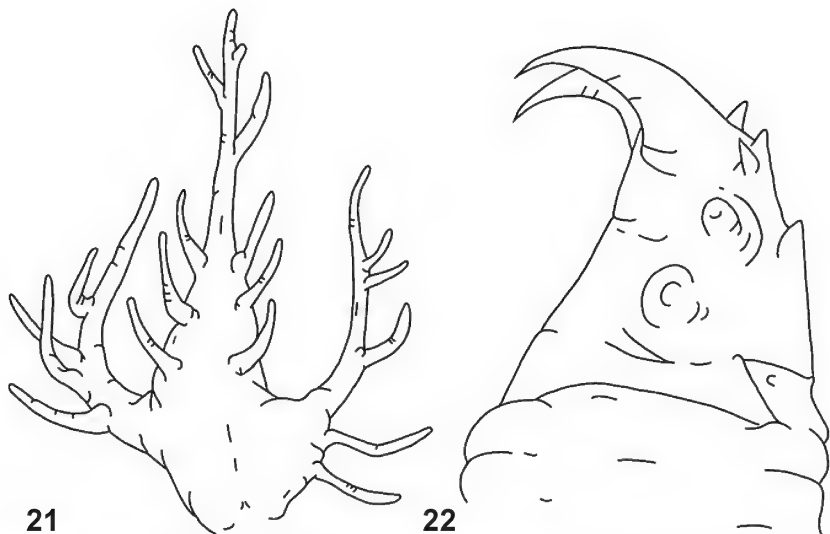
Abdomen with tergites dark brown, sternites yellowish brown. Hypopygium (Figs 12, 13) largely yellowish brown; posterior border of tergite 9 medially deeply and widely emarginate, notch semicircular, somewhat deepened in middle, lobes almost square and bearing abundant stout setae; gonocoxite rather slim, with rather large rounded mesal lobe; ventral branch of gonostylus with long apically rounded inner rostrum and strongly developed distinct outer lobe, dorsal branch slim, pointed and not strongly hooked; aedeagus long, conical, pointed; parameres long, subtriangular, with tip rounded.



Figs 17–20. *Dicranomyia (Idioglochina) caloundrae* sp. n., larva: (17–18) head capsule: (17) dorsal; (18) ventral; (19) mandible; (20) spiracular disk.

Male paratypes not differing significantly from holotype. Distance on costa between Sc1 and origin of Rs two-thirds to slightly more than whole length of Rs; basal section of R4+5 one-half to two-thirds length of Rs; R2+3 consistently strongly arcuated and m-cu slightly proximal to slightly distal to fork of M. Body length 5.5–7.5 mm. Wing length 7.8–10.0 mm.

Female (Fig. 14) with coloration and wing venation much the same as males, body length (excluding antenna) 5.0–6.7 mm, wing length 7.0–9.3 mm. Ovipositor

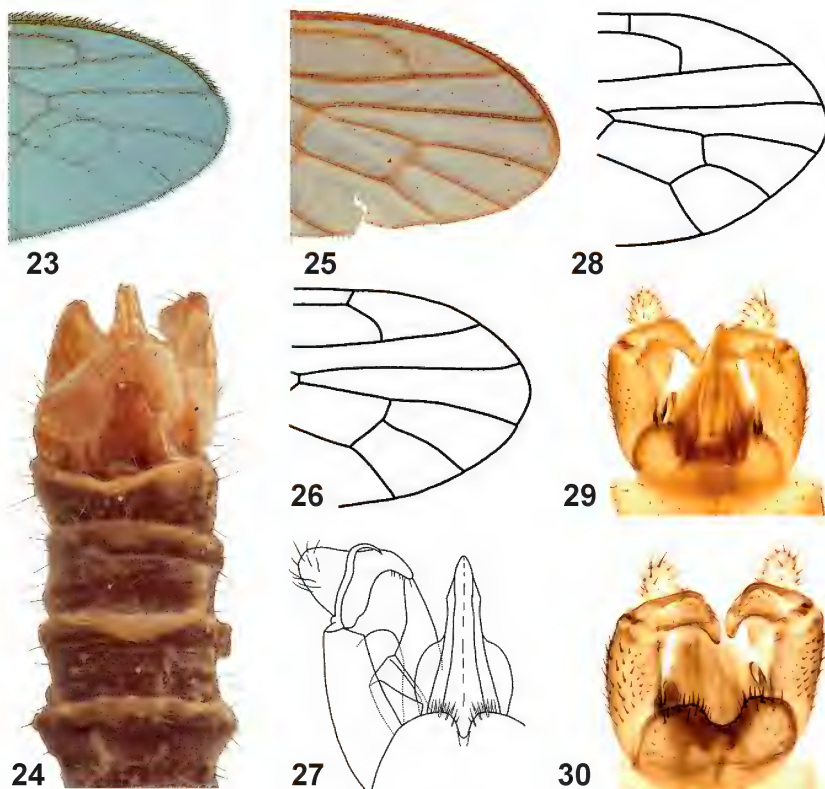


Figs 21, 22. *Dicranomyia (Idioglochina) caloundrae* sp. n., pupa: (21) respiratory horn; (22) cauda, lateral view.

with cercus slim, almost straight, markedly longer than tergite 10, but shorter than slim hypognathal valve (Fig. 15).

Larva (Figs 16–20)

Larvae cylindrical, 7.5 mm long. Pale white and smooth (dull pink in life), some sparse setae present but lacking obvious pubescence (Fig. 16). Dorsal and ventral creeping welts present on abdominal segments, each bearing minute spines. Head capsule coloured deep brown anteriorly, paling to golden brown in posterior half where sclerotisation is weaker, darkening to black in areas of heavy sclerotisation, particularly above eye spots at apices of the dorsal incisions and ventrally at fusion of genae and hypostomium (Figs 17, 18). Antenna short, cylindrical, with short terminal appendage. Clypeus with deep rectangular notch. Labrum a sclerotised plate, anterior margin shallowly concave, lateral margins rounded. Mandibles 4 toothed, second tooth larger than other teeth, with narrow dorsal ridge and molar surface minutely crenulate (Fig. 19). Maxilla fleshy with dense brush of setae on medial surface, cardo narrow elongate, palp short with sensilla terminal. Spiracular disc (Fig. 20) with five lobes, paired ventral and dorsolateral lobes short and broad, single dorsomedial lobe narrow and slightly longer. Dorsomedial lobe with heavy conical sclerite, coloured golden brown, extending from tip of lobe to centre of spiracular disk, sclerite bearing short tooth near its dorsal edge. Dorsolateral lobes bearing much weaker sclerites, pale yellow, ovoid, extending across dorsal 1/3 of lobe. Ventral lobes with similar weak yellow sclerites, broadly triangular and positioned in centre of lobes. Each spiracular lobe with



Figs 23–30. *Dicranomyia (Idioglochina)* spp., key characters. 23–24: *D. (I.) australiensis*; (23) wing tip, (24) abdomen, ventral. 25–27: *D. (I.) perkinsiana*; (25) wing tip, (26) wing tip, (27) male terminalia, dorsal. 28–30: *D. (I.) caloundrae* sp. n.; (28) wing tip, (29) male terminalia, ventral, (30) male terminalia, dorsal.

apical fringe of short setae, ventral and dorsolateral lobes each bearing single long thick seta. Spiracles in centre of disk, of moderate size, ovoid. Terminal segment ventrally bearing four short globose anal papillae.

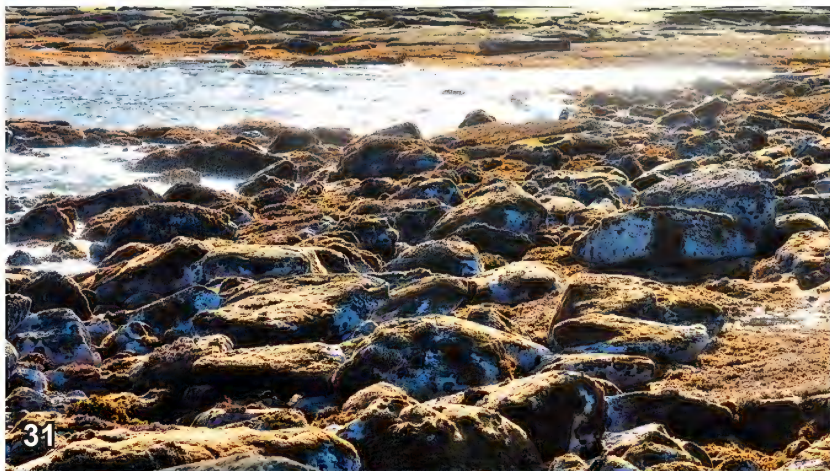
Pupa (Figs 21, 22)

General form elongate cylindrical, integument primarily smooth with five dorsal and ventral creeping welts present on abdominal segments, each bearing minute spines. Head, thorax and wing pads brown to dark brown, abdomen pale. Respiratory horns (Fig. 21) greatly developed, fleshy, with broad base dividing into three branches, each branch with numerous digitate projections. Central branch of respiratory horn consistently longer than lateral branches and generally equal to length of mesonotum. Number, length and placement of digitate processes vary

greatly between individuals. Wing pads not extending beyond first abdominal welt. Leg sheaths of equal length and not exceeding second abdominal welt. Cauda (Fig. 22) heavily sclerotised, bearing multiple rounded to low spinous lateral and ventral projections and two prominent dorsally curved hooklike projections.

Discussion. The adult of *D. (I.) caloundrae* (Figs 11–15) is very similar to both Australian species *D. (I.) australiensis* (Figs 2–6) and *D. (I.) perkinsiana* (Figs 7–10). The large size (male body 5.5–7.5 mm, wing 7.8–10.0 mm, female body 5.0–6.7 mm, wing 7.0–9.3 mm) clearly distinguishes it from *D. (I.) australiensis* (male body 4.5 mm, wing 4.8 mm, female body 4.5 mm, wing 5 mm). In addition, the aedeagus appears longer and more acutely pointed in male *D. (I.) caloundrae* (Figs 12, 13) than in *D. (I.) australiensis* (Fig. 6). A stronger arcuated R2 on the wingtip, the male terminalia with a wide, generally semicircular medially slightly deepened median notch of tergite 9, the outer portion of the ventral gonostylus narrowly produced and the dorsal gonostylus less strongly hooked (Fig. 12) distinguish it from the equally large *D. (I.) perkinsiana* in which R2 on the wingtip is only gently arcuated and in the male the median notch of tergite 9 is narrowly V-shaped, the outer portion of the ventral gonostylus not narrowly produced and the dorsal gonostylus more strongly hooked (Fig. 10).

Saunders (1928) provided the first account of the immature forms of *Dicranomyia* (*Idioglochina*), describing the larva and pupa of *D. (I.) signipennis* Coquillett, 1905, collected from marine algal growth on Newcastle Island, Vancouver, Canada. Alexander (1949) synonymised *D. (I.) signipennis* with *D. (I.) marmorata* Osten Sacken, 1861, which is distributed along the west coast of North America to California. Tokunaga (1939) then provided a description of the larva of *D. (I.) gloriosa* Tokunaga, 1938, found amongst marine algae on the shore of Sagami bay, Kanagawa, Japan. The descriptions by Saunders and Tokunaga provide the only points of comparison for the larvae of *D. (I.) caloundrae*, as no other descriptions of larval *Dicranomyia* (*Idioglochina*) seem to be available. Additional details of the pupa of *D. (I.) marmorata* were provided by Ring (1978) and included a thorough examination of the respiratory horns. The larvae of *D. (I.) caloundrae* were found living in marine algae, like the larvae of *D. (I.) marmorata* and *D. (I.) gloriosa*, and larvae are similar in general form. *D. (I.) caloundrae* seems more similar to *D. (I.) gloriosa* than to *D. (I.) marmorata* and the three species are readily distinguished by the features of the spiracular disk. *D. (I.) marmorata* possesses a spiracular disk with only 4 lobes, while both *D. (I.) gloriosa* and *D. (I.) caloundrae* possess a fifth dorsomedial lobe. In *D. (I.) caloundrae* the sclerite of the dorsomedial lobe bears a prominent tooth, while in *D. (I.) gloriosa* this sclerite lacks teeth or spines. No other Australian limoniid larvae are known to possess a spiracular disc with a conical sclerite bearing a tooth, and this feature readily distinguishes the larva of *D. (I.) caloundrae* from any other known Australian larvae. The pupae of *D. (I.) caloundrae* are generally similar to those of *D. (I.) marmorata* differing most noticeably in the development of the respiratory horn. In *D. (I.) marmorata* the respiratory horn has a single fleshy branch arising from a broad base, both lacking digitate processes, while in *D. (I.)*



Figs 31, 32. (31) habitat of *Dicranomyia (Idioglochina) caloundrae* **sp. n.** looking west in mid-afternoon; (32) a male perched in sunlight low on a boulder awaiting females with which to mate.

caloundrae three branches arise from the base of the respiratory horn, all bearing numerous digitate processes. The only other Australian pupae known to possess a multibranch respiratory horn are those of the genus *Antocha* Osten Sacken, 1861, however the number of branches is greater than in *D. (I.) caloundrae* and the branches do not bear digitate processes. Thus the structure of the respiratory horn easily distinguishes the pupa of *D. (I.) caloundrae* from any other known Australian limoniid pupae.

It should be pointed out that the species name *D. gloriosa* mentioned above in the discussion, turned out to be preoccupied and was replaced by the name *D. tokunagana* Alexander, 1964.

Etymology. Caloundrae is a toponym (noun in genitive case) referring to the type locality of the species near Caloundra in south-eastern Queensland.

Key to the males of Australian *Dicranomyia* (*Idioglochina*)

- 1 Small species, wing length approximately 5 mm; R2 long and strongly arcuated (Fig. 23); aedeagus blunt (Fig. 24); from Torres Strait, northern Queensland.....*australiensis*
Larger species, wing length 7–10 mm; R2 short and gently arcuated (Figs 25, 26) or long and strongly arcuated (Fig. 28); aedeagus pointed (Figs 27, 29); from eastern Australia.....2
- 2 R2 short and gently arcuated (Figs 25, 26); tergite 9 of male with narrow V- or U-shaped posteromedial notch (Fig. 27); from tropical eastern Australia.....*perkinsiana*
R2 long and strongly arcuated (Fig. 28); tergite 9 of male with wide, generally semicircular, posteromedial notch (Fig. 30); from sub-tropical eastern Australia.....*caloundrae* **sp. n.**

Biological observations

Habitat: Adults were found flying and perching in the lower intertidal zone. Although occasional specimens are seen around most rocky shores exposed to the ocean in the neighbourhood, the type locality, along about 200 m of shoreline, is distinguished by the way the rock shelf curves to face WSW, and is thus protected from most direct wave action from the Pacific Ocean. As a result of the calm conditions there has developed a broad expanse of shallow rock platform with low boulders supporting a rich growth of numerous types of marine algae, hard and soft corals and sponges which is exposed at low tide (Fig. 31). Adults are active in large numbers at low spring tides mainly along this favourable strip, usually within 20 m of the extreme low tide mark. The favoured breeding habitat appears to be thick encrusting mixed green and coralline algal mats on the top of low boulders. It was from these situations adults were seen emerging with the pupa embedded in the algal mat (Fig. 33). Young larvae were discovered in pure stands of pink *Corallina* alga growing lower in rock pools but only in small numbers and no mature larvae were recovered. Other marine Diptera present were one species each of *Clunio* Haliday and ?*Telmatogeton* Schiner (both Chironomidae). The

former were extremely numerous and their larvae dominated the *Corallina* beds.

Phenology: Daily counts were made for 41 days from June 26th to August 5th, covering one full lunar cycle from new moon to new moon. The tidal pattern is semidiurnal (i.e. two low and two high tides each 24 hours). Observations were made at the diurnal low tide, at that time of year the lowest tide of the day. On one day (22/7/2019) both low tides took place in twilight and no records



Figs 33–36. *Dicranomyia* (*Idioglochina*) *caloundrae* sp. n. adults, clockwise from top left: (33) a female emerging from pupa in algal mat; (34) adult resting under rock ledge; (35) adult perched in sunlight; (36) a female on top of an algal encrusted rock seeking an oviposition site.

were made. The results (Fig. 37) show a strong association with emergence and reproductive activity associated with lunar phases, with large numbers being present for 4 or 5 days around new moon and full moon. In this data set the lunar phase seemed more important in triggering emergence than tide level. Protandry was pronounced, with almost only males sampled on the first day of mass emergence. By the second day numerous teneral females were present as well as males with hardened bodies. Matings were observed. The following day oviposition began and numbers remained high for two or three more days, after which they disappeared. However the pattern of emergence varies seasonally, as has been shown for *Clunio tsushimensis* Tokunaga in the Sea of Japan (Saigusa & Akiyama 1995), where the tidal cycles are quite similar to Caloundra, with the lowest daily tide becoming nocturnal later in the year. Supporting this was the observation that no *D. (I.) caloundrae* were seen at a diurnal low tide of 0.04 m at new moon on 30/8/2019, about the time when the lower of the two daily low tides shifted to the night, and relatively few (15) were recorded on a standard transect walk at low tide (0.33 m) on the following full moon (14/9/2019). Both days offered perfect weather conditions. On 26–27/10/2019 (new moon) great numbers were observed near the nocturnal low tide just after midnight, whereas none were observed on the diurnal low, despite the tide falling to 0.23m. On 10–12/11/2019 and 10–12/12/2019 (full moon) the same pattern occurred. On 25–26/11/2019 (new moon) very large numbers were present at night, whereas only a small number were active (5 detected on a standard transect walk) during the diurnal low (0.33m). At night the insects were detected by illuminating the main habitat with car headlights. It was not possible to establish counts comparable with the diurnal observations shown in Fig. 37, but the general impression was that peak numbers were similar. These observations further indicate that emergence and activity are not linked to the absolute level of the low tide, but are synchronised to the lower of the two tides each day around full and new moon.

Behaviour: Adults were observed on the wing, mating and ovipositing. Sometimes they rested on algal mats on boulders in sunlight, especially on windy days, and occasionally under rock ledges (Figs 32, 34–36). They were active even on dull days and in light rain. Females especially were observed emerging from their pupae embedded in algal mats (Fig. 33) and on three recorded occasions a male stood over the emerging female and mated with her once she emerged. On another occasion, two males contested possession of an emerging female and a fight ensued with both flying out of sight and the female emerged unhindered. Most matings probably took place when males located post teneral females. Oviposition was observed frequently. The female would perch on top of an algal mat on a low boulder, often washed by waves, and rapidly bob up and down as she inserted her ovipositor into the substrate in quick short stabs. Sometimes a male would stand over her, almost certainly a case of mate guarding, and on six occasions determined efforts were made by a second and twice by a third male to displace the guarding male, none of which were successful although two struggles resulted in all three males flying off leaving the female unguarded. Attempted mating with

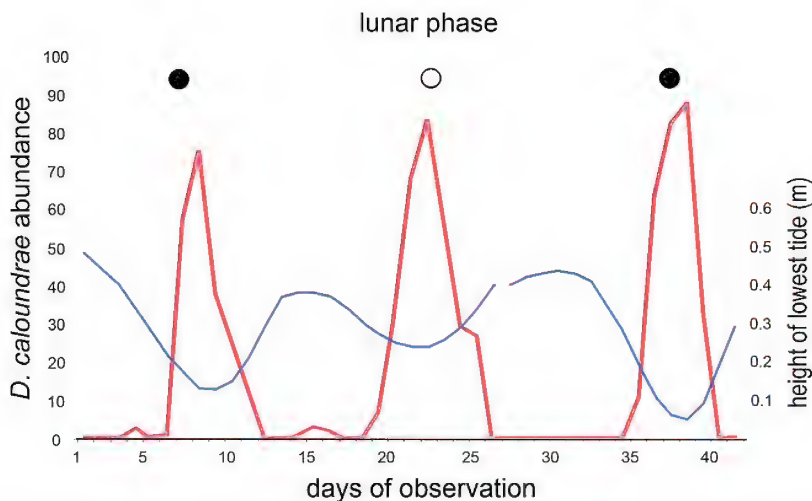


Fig. 37. Phenology of appearance of *Dicranomyia (Idioglochina) caloundrae* sp. n. adults (red line, relative abundance scale left abscissa) and lowest daily tide (blue line, tide level scale right abscissa) from 26/6/2019–5/8/2019; lunar phase indicated above.

ovipositing females was observed several times but was never successful.

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The map provided in Fig. 1 is modified from SIO, NOAA, U.S. Navy, NGA, GEBCO map data, created using Google Earth Pro for desktop, © Google 2019.

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**PSEUDOFOENUS ALBICOLEUS SP. N., A HYPTIOGASTRINE
PREDATOR-INQUILINE OF THE COLLETID BEE *LEIOPROCTUS*
(*GONIOCOLLETES*) *WANNI* (LEIJS & HOGENDOORN, 2016)
FROM SOUTH-WEST WESTERN AUSTRALIA**

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Key words: taxonomy, new species, Gasteruptiidae, Hyptiogastrinae, immature stages, Colletidae

Abstract

Pseudofoenus albicoles sp. n., is a new species of hyptiogastrine wasp from south-west Western Australia. It has been reared from nests of the ground-nesting colletid bee *Leioproctus* (*Goniocolletes*) *wanni* (Leijs and Hogendoorn, 2016). We provide details and images of immature stages of the wasp.

Introduction

The Gasteruptiidae is a distinctive family of parasitic wasps easily recognised by their slender, subclavate metasoma inserted very high on the propodeum, the elongate, neck-like propleura and clavate hind tibia (Crosskey 1953, 1962; Jennings & Austin 2002). The family is divided into two monophyletic subfamilies, Hyptiogastrinae and Gasteruptiinae (Jennings & Austin 2000, Parslow *et al.* 2020a). The Hyptiogastrinae comprise two genera (*Hyptiogaster* Kieffer, 1903 and *Pseudofoenus* Kieffer, 1902) and includes 11 and 78 species, respectively, that are almost entirely from Australasia (Australia, Fiji, New Zealand, New Guinea, New Caledonia and Vanuatu), except for two species in South America (Jennings & Austin 2002; Parslow & Jennings 2018).

For the majority of *Pseudofoenus* species, little is known about their hosts (Jennings & Austin 2004, Grieve *et al.* 2018), although available records indicate they are predator-inquilines of ground-nesting bees. This paper describes a new species of *Pseudofoenus* that has been reared from nests of the ground-nesting bee *Leioproctus* (*Goniocolletes*) *wanni* (Leijs and Hogendoorn, 2016) (Colletidae) (see Houston 2020).

Materials and Methods

Terms for general morphology follow Jennings & Austin (2002), and that for wing venation follows the modified Comstock-Needham system after Sharkey (1988) but with some modifications, and using the nomenclature of van Achterberg (1979) for cells (see also Jennings & Austin 2002). Terms for surface sculpturing follow Harris (1979). Where measurements are based on more than one specimen, data are presented as the mean followed by the range. Measurements were taken with a Nikon SMZ1500 stereo microscope at the South Australia Museum. Images



Figs 1, 2. *Pseudofoenus albicoleus* sp. n., holotype female, (1) lateral habitus, (2) dorsal habitus. Scale bars = 1.0 mm.

were taken using a Visionary Digital LK imaging system (Dun, Inc.) with Canon EOS 5DsR camera using Zerene Stacker 1.04 software (College of Science and Engineering, Flinders University, South Australia). The following abbreviations are used for the depositories; SAMA = South Australian Museum, Adelaide, South Australia; WAM = West Australian Museum, Perth, Western Australia.

Pseudofoenus Kieffer, 1902

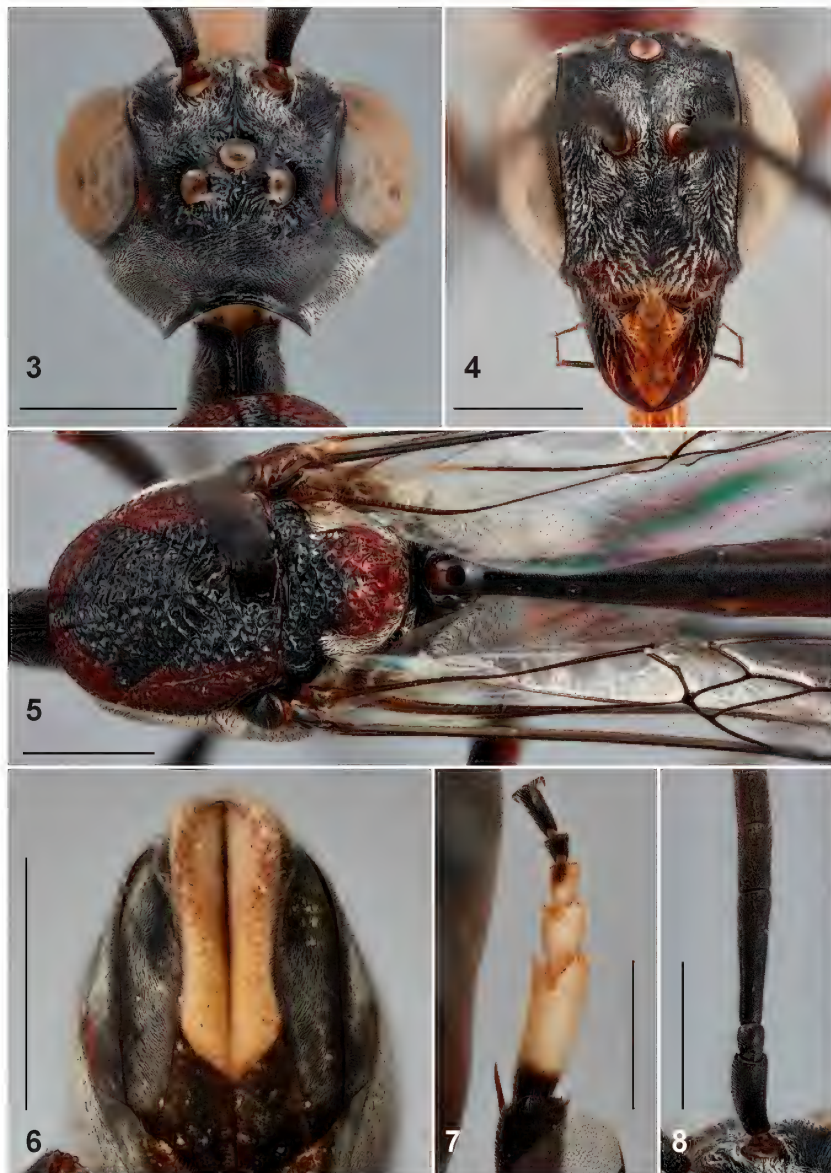
Comments. For a detailed synopsis and discussion of the genus, see Jennings & Austin (2002).

Pseudofoenus albicoleus sp. n.

(Figs 1–12)

Type material. *Holotype* ♀, WESTERN AUSTRALIA: Corackerup Creek c. 44 km SSW of Jerramungup, W.A., 34°18'14"S, 118°43'36"E, 26–28 January 2019, T.F. Houston 1542-2b, flying close to ground at nesting site of bee, *Leioproctus* (*Goniocolletes*) *wanni*, in kaolin exposure at breakaway (WAM: E101588).

Paratypes. 3♀♀, same data as holotype (WAM: E101589, E101590, E101594); ♀, same data as holotype, T.F. Houston 1567-1, in ethanol (SAMA: 32-035930); 3♂♂, same data as holotype (WAM: E101591, E101592, E101593).



Figs 3–8. *Pseudofoenus albicoles* sp. n., holotype female. (3) dorsal head; (4) frontal head; (5) dorsal mesosoma and metasomal T1; (6) ovipositor sheath; (7) dorsal hind tarsus; (8) dorsal right antenna. Scale bars = 1.0 mm.



Figs 9–11. *Pseudofoenus albicoles* sp. n., predefecating larva. (9) ventral habitus; (10) dorsal habitus; (11) lateral habitus. Photo credit T.F. Houston 2019.

Description. Female (Figs 1–8). Length 16.2 (15.8–16.8) mm. **Colour:** Body black and dark brown, head black, except lateral corners of clypeus and malar space dark brown, face and frons with silvery pubescence, small brownish spot on eye margin in line with posterior ocelli, hind tarsomere 1 whitish in apical $\frac{3}{4}$, tarsomere 2 entirely white, tarsomere 3 largely white except for small patch of black dorso-apically, tarsomeres 4 and 5 with small amount of white apically, apical margin of tergite 9 white, ovipositor sheaths white (Fig. 6). **Head:** Wider than long when viewed dorsally (Fig. 3); face and frons rugose, some shallow punctures along eye margin; frontal median carina pronounced (Fig. 4); vertex mostly rugulose, with fine lateral striations, several punctures near ocelli, with short setae; gena imbricate, pubescence long; occipital carina broad, smooth; malar space $0.05\ (0.03\text{--}0.07) \times$ height of eye; clypeus $1.5 \times$ as wide as high, imbricate, anterior margin sinuate, weak medial carina present; distance from lateral ocellus to eye margin $0.7\ (0.6\text{--}0.8) \times$ distance between lateral ocellus and occipital carina; scape $3.1\ (2.8\text{--}3.2) \times$ length pedicel; first flagellomere $1.4\ (1.3\text{--}1.5) \times$ as long as scape, $2.0\ (1.9\text{--}2.1) \times$ as long as second flagellomere; mandible with two blunt medial teeth (Fig. 4). **Mesosoma:** Propleuron imbricate, with a few shallow punctures, ventro-lateral carina absent, pubescent, less dense dorsally; lateral pronotum weakly imbricate, almost smooth in dorsal part, ventral part imbricate; medial and lateral lobes of mesoscutum rugose-areolate, with scattered short setae, notaulus carinate, parapsidal line distinct, medial line distinct (Fig. 5); scutellum and axilla rugose, several punctures on axilla; metanotum rugose; mesepisternum with long dense pubescence, dorsal part rugose, separated from ventral part by carinate depression, ventral part rugose; mesepimeron broad, carinate; metapleuron with long dense pubescence, dorsal part rugose, ventral part strigate-rugose; propodeum areolate, propodeal spiracle



Fig. 12. *Pseudofoenus albicoleus* sp. n., pupa, lateral habitus. Scale bar = 1.0 mm.

elongate; hind coxa strigate dorso-apically, remainder imbricate, pubescence long laterally; hind trochanter with groove on inner surface, imbricate, pubescence short; hind femur imbricate, pubescence short; hind tibia imbricate, pubescence short, with scattered emergent stout setae; hind femur $4.9 (4.2-5.3) \times$ long as wide, $0.8 \times$ length hind tibia; hind tibia with ventro-apical pecten of short robust spines; hind tarsomeres 1–4 with ventro-apical pecten of short robust spines, hind tarsomeres 1 and 2 slightly asymmetrical, with stout setae on ventral surface (Fig. 7), tarsomere 1, $2.1 (1.8-2.4) \times$ length tarsomere 2; tarsomere 2, $1.7 (1.5-1.9) \times$ length tarsomere 3; tarsomere 3, $1.5 (1.2-1.8) \times$ length tarsomere 4; tarsomere 4, $0.5 (0.5-0.6) \times$ length tarsomere 5; hind tarsal claw (Fig. 7) $0.7 (0.6-0.7) \times$ as long as tarsomere 5; hind wing venation complete, veins 1-M and 2M+Cu tubular, remainder spectral; hind wing with 3 hamuli. **Metasoma:** $2.7 (2.7-2.8) \times$ length of mesosoma; T1 imbricate, with a few shallow punctures dorso-laterally, longitudinal median ridge absent (Fig. 5).

Male. Similar to female except length 16.1 (14.8–17.4) mm; hind tarsomere 4 lighter brown; basiparameres with cream spot on apex.

Larva. A single larva was excavated from a host brood cell 26.x.2019 (Figs 9–11). It was at a post-defecating stage based on the absence of the host larva and/or cell provisions and the presence of a meconium (see Houston 2020, this issue).

Larva rotund, wide and stout, length $1.9 \times$ longer than wide, well developed body segments of similar width (Fig. 10). Simple erect setae abundant on elevated dorsal and lateral surfaces of mesosoma and metasoma, becoming scattered on ventral surfaces (Figs 9–11). Head small in relation to body size; oriented in normal, hypognathous position relative to thorax (Fig. 9). Head capsule unpigmented except at mandible apex and faintly pigmented on anterior margin of labrum.

The larva pupated between 15–25.xi.2019.

Pupa. Pupa exarate, resembling a “mummified” adult, 13.4 mm in length, cream with red eyes. Cuticle largely sclerotised by 8.xii.2019 (Fig. 12) and eclosed as an adult 15–16.xii.2019.

Etymology. The species name is derived from a combination of the Latin *albus*, for white or whitish and *coleus*, for sheath or scabbard, in reference to the white ovipositor sheaths.

Comments. Using the key of Jennings & Austin (2002), *P. albicoles* runs to the *P. macronyx* group (couplet 5) based on the presence of hind wing vein 1-Cu. The *P. macronyx* group comprises three species, *P. grossitarsis* (Kieffer), *P. houstoni* (Jennings and Austin) and *P. macronyx* (Schletterer), all endemic to Western Australia (Jennings & Austin 1994, 2002). However, these species all have a subapical notch on the inner surface of the mid tibia of females which is lacking in the new species.

The female of this new species can be readily identified by the distinctive white ovipositor sheaths.

There is extremely limited information on larvae of *Pseudofoenus*, with the majority of described larvae being of Gasteruptiinae (e.g., Malyshev 1966, Bogusch *et al.* 2018, Parslow *et al.* 2020b). The larvae of *P. albicoles* can be easily distinguished from those of *Gasteruption* Latreille based on a wide and stout body shape, and the absence of paired body tubercles on metasomal segments (Bogusch *et al.* 2018).

Jennings & Austin (1997) described the exarate pupae of *P. thoracicus* (Guérin-Ménéville, 1843), but unlike the pupae of this species, the pupa of *P. albicoles* has very long setae on various body parts, e.g. eye and hind tibia of the pupa (Fig. 4). They are shed when the adult ecloses (Fig. 1).

Acknowledgements

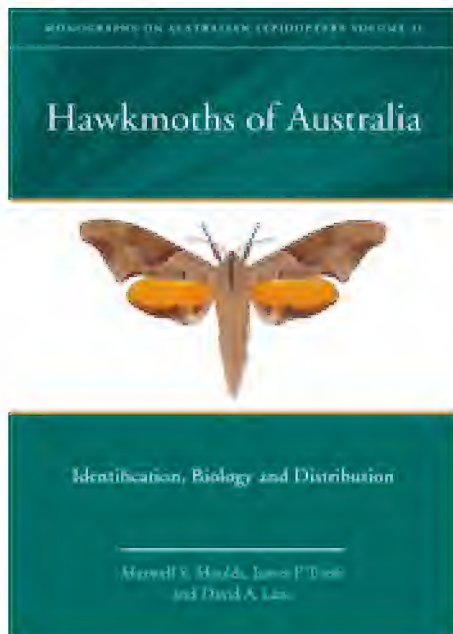
We are grateful to Terry Houston (Western Australian Museum) for making available to us specimens of adults, a larva, and imaging the larva for Figs. 9–11. We would also like to thank Nik Tatarnic (Western Australian Museum) for facilitating examination of material held at the Western Australian Museum. We wish to thank Cornelis van Achterberg (Naturalis Biodiversity Center) and Giuseppe Fabrizio Turrise (University of Catania) for their kind reviews.

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BOOK REVIEW

Hawkmoths of Australia. Identification, Biology and Distribution. Monographs on Australian Lepidoptera Volume 13, by Maxwell S. Moulds, James P. Tuttle and David A. Lane. CSIRO Publishing, Melbourne. ISBN: 978 1 486302 819. 424 pages



This long awaited monograph of the Australian hawkmoths has, in every sense of the word, certainly been worth waiting for, as a quick perusal of the book reveals to anyone in the scientific community, or interested collector, that this is truly a very special and much needed publication on one of the most widely worked groups of moths in the world, the Sphingidae.

As I began reading through the entire book, which actually took several weeks, it was immediately apparent that there is an astonishing wealth of new, previously unpublished information available nowhere else and is clearly the culmination of years of extensive fieldwork.

To begin, the Acknowledgments section is very extensive, and clearly indicates just how much

emphasis was placed by the authors on gathering as much data as possible from a substantial number of additional experts dealing with sphingids in Australia and overseas.

In the Organisation and Presentation section it is important to note how the authors used DNA barcode sequences in BOLD (Barcode of Life Data Systems project) to compare taxa, assess allopatric populations within species complexes and genetic diversity within single populations that exhibited distinct morphological variation. This made it possible for the authors to identify adults in difficult species complexes such as the genus *Psilogamma* and associate their larvae successfully for the first time. Importantly, some twenty taxonomic changes are also noted in this section.

The Structure and Function chapter has to be seen to be believed. Apart from the extremely detailed text it contains 43 beautifully executed figures of the adult body, wings, male and female genitalia, larva and pupa. The extraordinary number of named structural parts must make this the most detailed overview of

hawkmoth morphology since Rothschild and Jordan (1903). To my knowledge the figure of the complete female reproductive system is the first ever published for a hawkmoth. There are other chapters on collection and preservation, rearing hawkmoths, and a detailed account of hawkmoth biology.

The remaining chapters are where this book really excels. The attention to detail is nothing short of astounding and it becomes very clear why this book took so long to reach publication. Years of careful study, collection and recording of data for the egg, larva, pupa and adult stages of each species have provided the foundation for the remainder of the book.

The Australian fauna chapter opens with a checklist of the Australian species which includes species from the Australian mainland, Tasmania, Torres Strait, Christmas Island and Cocos-Keeling Islands. It is both interesting and very pleasing to see well-thought out keys to last instar larvae and pupae. In fact, I have never seen keys like these published in a sphingid book before and I doubt it would be possible to identify the hawkmoth pupae without that key.

The life histories are documented in almost extreme detail in most cases for 70 of the 87 known species. It should be noted that 25 life histories are completely new and the majority of the others were previously known mostly from only the last larval instar. This is a remarkable achievement for the authors considering that of the 17 species not documented, 6 are known from single Australian specimens and 7 others from fewer than 10 specimens. Even the two iconic Australian species *Coequosa australasiae* and *C. triangularis* are documented accurately for the first time. The book also notes that 5 species are recorded from Australia for the first

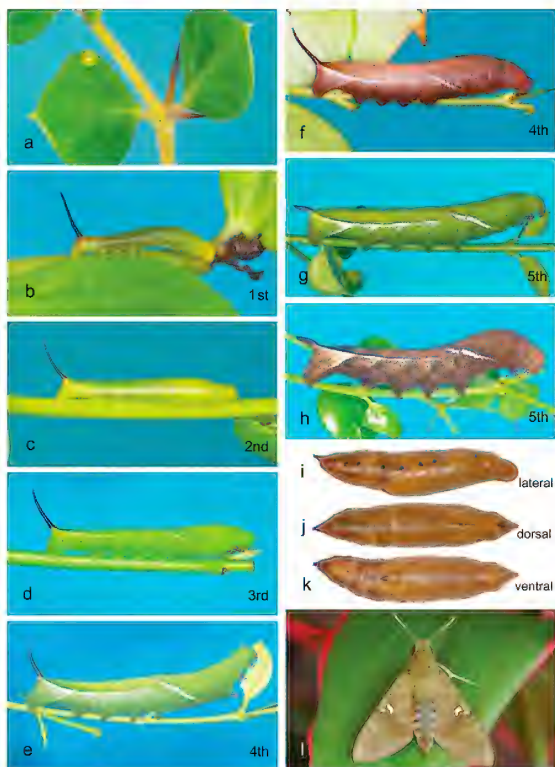


Plate 52 from *Hawkmoths of Australia* showing life stages of *Nephele subvaria*.

time. One species described, *Macroglossum queenslandi*, must truly illustrate the thoroughness of the authors in their quest for new life histories. First found in the early 1900's but not recorded again for over 100 years until the authors not only rediscovered the species but documented its life history.

The distribution maps for each species use the dot technique to show exact location records. This is much more accurate than in publications that shade whole areas as many of the species recorded often have very localised ranges specific to their foodplants. Regarding the foodplants, while many of these have been previously recorded many new ones are recorded here, in addition to making corrections to some previously published.

The array of images of larval instars and pupae contained in Plates 4–72 are simply unmatched in any previously published work. Even the pupae are shown in lateral, dorsal and ventral views.

Significantly, the male genitalia are figured for all species, and nearly all for the first time, in Plates 84–92. The fact that they are all illustrated from the same position makes comparisons much easier than many publications that often figure male genitalia from different angles.

In Appendix 1 the authors have produced a remarkable list of Sphingidae parasitoids. More than 90% of these records are new to science. New parasitoids are recorded for an astonishing 43 species, previously known for only 11 species.

Appendix 2 provides a very detailed summary of known larval foodplants. Upon reading through this section it is interesting to note that many hawkmoth species have adapted to a wider variety of foodplants than one would expect.

Apart from the Index, the book finishes with a substantial References section that includes numerous, but important, obscure references. This partly annotated section of the book is of particular value to researchers working on hawkmoths.

If one is to find fault with this work then it would be in the printing of the plates depicting set adults (Plates 73–82) where some are unfortunately slightly darkened, particularly evident in Plate 76 of the *Macroglossum* images. This is rather surprising given the high level of technology employed in the printing industry these days.

This magnificent reference book is available in hardback through CSIRO Publishing at a cost of AUD\$220. Given the enormity of information in this publication in both text and plates and the current cost of most similar quality scientific books, this is a reasonable price, for a book that is utterly indispensable to any researcher working in this field either in Australia or overseas. This monograph sets a new benchmark for all future similar publications. The authors are to be congratulated for all their efforts in producing this truly magnificent book.

Reviewed by Robert B. Lachlan

ON THE NESTING BIOLOGY OF A SOLITARY BEE IN THE SUBGENUS *LEIOPROCTUS* (*GONIOCOLLETES*) (HYMENOPTERA: COLLETIDAE) IN SOUTH-WESTERN AUSTRALIA

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Key words: Apoidea, ethology, burrowing, gregariousness, *Eucalyptus*, new combinations

Abstract

Despite the large size and diversity of the bee genus *Leioproctus* Smith, 1853 and the abundance of many of its species, few detailed accounts of nests of this taxon appear in the literature. Here, details are provided of a highly populous, perennial nesting aggregation of *L. (Goniocolletes) wanni* (Leijs & Hogendoorn, 2016) **comb. n.** in a kaolinite exposure bordering a creek in south-western Australia. This is the first account of nests for the subgenus *Goniocolletes* Cockerell, 1907. Cell form was largely typical of *Leioproctus* and the larval provision (judging from failed cells) was a formed, rounded pollen mass. Two species of parasitoid wasps, *Pseudofoenus albicoles* Parslow & Jennings, 2020 (Gasteruptiidae) and *Ephutomorpha* sp. affin. *morosa* (Westwood, 1843) (Mutillidae), were very abundant over the nesting site and evidence of them was found in brood cells.

Introduction

The genus *Leioproctus* Smith, 1853, which is represented across Australasia and temperate South America, is extremely diverse. In Australia, there are over 200 named species which were divided among 16 subgenera by Michener (2007). Subsequently, seven new subgenera were added (Houston and Maynard 2012; Maynard 2013). Many species are quite common and yet very few have been studied in any detail. The published accounts of nesting biology represent few of the known subgenera (for a summary see Maynard 2013). Nothing has been published hitherto on the nesting biology of members of subgenus *L. (Goniocolletes)*. This taxon was arbitrarily accorded generic status by Maynard (2013), so it is of interest to gain some knowledge of its nesting biology.

When last revised (Maynard 2013), *Goniocolletes* Cockerell, 1907 comprised 14 species. Maynard noted that “The genus appears widespread in Australia although no specimens have been taken in the northern parts of the country or along the very well-collected east coast. Most species have been collected at blossoms of Myrtaceae, especially of *Eucalyptus* in drier areas.” Leijs and Hogendoorn (2016) described an additional species, *G. wanni*, from southern South Australia and southern Western Australia. It is this species that forms the subject of the present paper.

The nesting site reported here was brought to my attention in February 2011 by Michael Davis (pers. comm.), who reported the bees entering and leaving holes in white clay at a ‘breakaway’ on Corackerup Creek, a site located approximately 44 km SSW of Jerramungup in southern Western Australia. Photographs and videos of bees taken at the site by Mr Davis revealed what appeared to be both sexes of a *Leioproctus (Goniocolletes)* species. In January 2018, Dr Eddy Wajon sent me images of what appeared to be the same bee species and it transpired that they

were taken at the same site and time as Mr Davis's, the site being accessed via Chingarrup Private Sanctuary, the property of Dr Wajon and his wife Donna. I visited the nesting site first in late January 2019 (when adult bees were active) and again in late September 2019. The observations made on those two occasions and on material returned to the laboratory are recorded here.

Materials and Methods

The nesting area was accessed via a four-wheel drive track and then a walk of about 500 m over rocky ground in densely wooded habitat along the creek margin. This limited the amount of equipment that I could carry in.

During the period 26–28 January 2019, I visited the nesting site three times on consecutive days between the hours of 10.00 am and 5.00 pm when conditions were favourable for bee activity (cloudless sky, light breeze, air temperature 30–37°C and nesting site fully exposed to sun). On 26 September 2019, the nesting site was revisited in order to excavate brood cells containing live stages.

In January, using a spade and trowel, two small excavations *c.* 30 cm x 30 cm in area and *c.* 30 cm deep were made at the site where the ground slope was *c.* 30°–40°. Some blocks of kaolinite (totalling *c.* 1.5 litres) were cut for later examination in the laboratory. In September, a larger and deeper excavation was made adjacent to the earlier ones and a block of *c.* 7.5 litres was removed for later study.

The bee species forming the subject of this article was at first identified as *Goniocolletes comatus* Maynard, 2013 using Maynard's (2013) revision of *Goniocolletes*, the male terminalia closely matching those in her figures 205–207. However, in the opinion of Leijs and Hogendoorn (2016), Maynard based her description on specimens of two very similar species and the male terminalia were not of the nominal species. Leijs and Hogendoorn recorded *G. comatus* only from the Flinders Ranges and northern Eyre Peninsula, South Australia, whereas their new species, *G. wanni*, was recorded widely from southern Australia, east and west of the Nullarbor Plain. High-resolution images of both sexes of the bees collected from the nesting site on Corackerup Creek were sent to Remko Leijs (South Australian Museum) who agreed that the species was almost certainly *G. wanni*, despite females being slightly atypical. In keeping with my previously expressed view that *Goniocolletes* does not warrant generic status (Houston 2018, p. 109), I am here retaining it as a subgenus of *Leioproctus* (as in Michener 1965, 2007). Accordingly, I here record Maynard's (2013) seven new species and Leijs and Hogendoorn's (2016) one new species as new combinations in *Leioproctus*.

Specimens of a gasteruptionid wasp collected over the bee nesting aggregation were forwarded to John Jennings (University of Adelaide) and Ben Parslow (South Australian Museum) for identification. Christopher Taylor (University of Western Australia) was sent a high-resolution image of one of the mutillid males from the nesting site. Specimens of *L. wanni* and associated parasitoids collected at the nesting site as well as specimens of the bee collected from flowers on Chingarrup Sanctuary are lodged in the Entomology collection of the Western Australian Museum.



Figs 1, 2. Nesting area of *Leioproctus* (*Goniocolletes*) *wanni* at the 'ochre cliffs', Corackerup Creek, south-western Australia. (1) View over kaolinite exposure on south bank of creek looking east (nesting area arrowed); (2) closer view of nesting area (burrows were observed throughout the sloping foreground). Photos: Graeme Zemunik.

Observations

Nesting site

The nesting aggregation was situated in a section of breakaway approximately 300 m long that margined Corackerup Creek, c. 44 km SSW of Jerramungup (-34.29° , 118.70°) (Fig. 1). In January, intense bee activity was observed to be confined to a relatively small part of the breakaway, an amphitheatre-like section that measured c. 15 m x 8 m and which was composed of white and pinkish-orange kaolinite (Fig. 2). Originally, this soil horizon would have been overlain by reddish, iron-rich clay topped in turn by hard lateritic duricrust (visible to the right in Figs 1, 2).

Judging by the numbers of small holes and the bees hovering over them, thousands of active nests were present in this area.

Adult activity

On each visit to the site in January, thousands of bees were milling about over the sloping ground generating a very audible hum. Some females were observed to enter burrows bearing pollen loads on their hind legs, but most carried no pollen and appeared to be searching the site, frequently entering holes, only to reappear within several seconds and moving on. Males made up a large proportion of the hovering contingent. A small sheoak at one side of the nesting area was patrolled by a persistent swarm of flying males that kept mainly to its leeward side. Many mallee-form *Eucalyptus* trees (notably *E. phaenophylla* and *E. vegrandis*) were in flower in the bushlands adjacent to Corackerup Creek in January and a few males of *L. wanni* were collected from flowers of the former c. 2.5 km from the nesting site.

No adult activity was observed in September.

Nest structure

Numerous simple holes were observed in the kaolinite in January and none had a well-developed tumulus. However, some loose, dry soil was present down-slope from some of them. Where excavations were made at the edge of the nesting aggregation, a thin veneer of loose sand covered pinkish-white clay that contained numerous rust-coloured, stony, crystalline inclusions making it very difficult to follow individual burrows that wound around and between them. This clayey ground was quite solid, so that blocks of it could be cut and removed.

Dozens of old, vacated and mostly soil-filled cells were encountered within the first few centimetres of consolidated clay down to a depth of c. 40 cm (measured perpendicular to the sloping surface). Cells containing live stages were only found below c. 27 cm. Cells were elongate-ovoidal with the floor flatter than the ceiling, thus being bilaterally symmetrical (Fig. 3). Their long axes were horizontal or inclined up to c. 30° . Based on a few selected examples, maximum diameters of cells ranged from 7.2–7.7 mm and lengths from 15.5–17.7 mm. Diameters of cell mouths (= diameters of cell plugs) ranged from 3.2–4.7 mm.

Cells occurred singly or side by side and no linear series were found. The inner



Figs 3, 4. *Leioproctus (Goniocolletes) wanni*: (3) brood cell opened laterally showing prepupa and meconium; (4) prepupa.

soil surfaces of the ovoidal cells were extremely smooth but did not appear to be built in. They were lined with an extremely thin, cellophane-like membrane which could be peeled off only in tiny fragments. Cell plugs were rather rough on their inner surfaces, strongly concave centrally, and seemingly comprised of a single whorl, plugged centrally. They were indistinguishable from the barricades filling the access burrows. In most cells examined, a thin meconium was situated in the upper, inner end and consisted of overlapping, somewhat flattened, linear faeces (Fig. 3).

No freshly constructed, provisioned cells were encountered in either the January or September visits. However, a few old, sealed cells were encountered in which were found the mouldy remains of pollen provisions. In each case, the depressed ball-shaped mass (maximum diameter 4.7 mm) sat on the floor of the cell at its inner end. These provisions consisted of triangular pollen grains, consistent with being those of *Eucalyptus*.

In January, cells containing a live prepupa, a pupa and a freshly eclosed male adult were exposed in the deepest part of one excavation. In September, the only live stages found were prepupae (Figs 3, 4), 20 being sampled.

Parasitoids

In January, the nesting site was patrolled by numerous males and females of the gasteruptiid wasp, *Pseudofoenus albicoles* Parslow & Jennings, 2020 and males of a mutillid wasp (Fig. 5), provisionally identified as *Ephutomorpha* species *cf. morosa* (Westwood, 1843) (Christopher Taylor, pers. comm. 2019).

No evidence of parasitization by the gasteruptiid was found among the many brood cells collected in January, but a cell taken in September contained a rotund, bristly larva considered likely to be that of *P. albicoles*. It rested on a blackish meconium in the floor of the cell. Two cells found in January and one found in September contained cocoons likely to be those of Mutillidae (Fig. 6). One cocoon was open and sand-filled while two were entire. One closed cocoon contained only a mouldy object, presumably the shrunken remains of the occupant larva, and the other was not opened.

Discussion

Given that nesting activity of *L. wanni* was observed at the Corackerup Creek site in 2011 and again in 2019, it was evident that the nest aggregation was a perennial one. The strongly sloped surface of the ground there was eroding, so presumably each generation of the bees made its brood cells a little below those of the preceding one, accounting for why old, vacated cells occurred from just beneath the surface to a depth of c. 50 cm, yet cells containing live stages were found only below c. 27 cm. Clearly, the nesting site had been used by many generations of bees.

Kaolinite is a layered silicate clay mineral which forms from the chemical weathering of feldspar or other aluminum silicate minerals (Abeyasinghe and Fetherston 1999). Exposures are not commonplace and would not be found



Fig. 5. Male of *Ephutomorpha* sp. found flying over nesting area of *Leioproctus* (*Goniocolletes*) *wanni* at Corackerup Creek.



Fig. 6. Cocoon presumed to be that of a mutillid parasitoid removed from a brood cell of *Leioproctus* (*Goniocolletes*) *wanni*.

throughout the range of *L. wanni* which covers much of the ‘mallee’ *Eucalyptus* belt of southern WA and SA (Leijs and Hogendoorn 2016), so kaolinitic clay is unlikely to be the usual nesting medium. However, the enduring presence of the Corackerup Creek nesting population at least points to clay soil being the most likely medium.

At the time of my January visit, it appeared that nesting was in its early stages, with more females hovering over and searching the ground than entering burrows laden with pollen. Consequently, most of the holes observed were probably emergence holes. The bee’s activity coincided with the flowering of mallee-form *Eucalyptus* species in the area and this observation is consistent with the floral records noted for *L. wanni* by Leijs and Hogendoorn (2016).

The few cells found to contain late immature stages and young adults during my January visit were almost certainly constructed in the previous summer. My failure to find freshly provisioned cells in January was probably because I did not excavate deep enough. Judging by a few mouldy cells, though, the provision is a solid, rounded mass which would be consistent with all previous records of provisions for *Leioproctus* (Houston & Maynard 2012; Maynard 2013; Michener 1960; Michener & Lange 1957). The mostly horizontal orientation of the cells of *L. wanni* also suggests solid provisions as paracolletines (*sensu* Michener 2007) that have a liquid provision construct vertical or strongly inclined cells (Houston 2018, 2020).

Cell plugs of ground-nesting bees typically show a concave spiral pattern on the inner surface (Stephen *et al.* 1969). Unfortunately, there are few published descriptions of cell plugs of *Leioproctus*. Maynard (2013) described that of *L. (L.) nigrofulvus* as “an unlined, oblique disc-like plug”. Those of *L. wanni* were found to have a rather rough but concave inner surface lacking a spiral pattern. Given that the cell mouths were relatively narrow, only just wide enough to permit passage of the females, it may have been impractical for the bees to build spiral closures.

Faecal deposits of Australian paracolletines have seldom been described. Maynard (2013) noted for *L. (L.) nigrofulvus* (Cockerell, 1914) that “a disc of faeces was found plastered in slender strips over the plug-end of the cell.” In my experience, this is highly unusual as faeces are usually deposited in the inner (basal) ends of cells.

Despite the abundance of two parasitoid wasps, *Pseudofoenus albicoles* (Gasteruptiidae) and *Ephutomorpha* André, 1902 species (Mutillidae) over the nesting area in January, just a few of the cells excavated showed evidence of parasitisation by them. The single larva presumed to be that of the former wasp rested on its own meconium and the absence of a host meconium in the cell suggests that the larva fed on the host provision (i.e. it was a cleptoparasite). By contrast, all three cells containing cocoons presumed to be those of mutillids also

contained a typical host bee meconium, suggesting that the mutillid larvae fed upon the mature bee larvae. This would be consistent with what is recorded of mutillid life-histories (Brothers 1972; Hearn *et al.* 2019). There are no previous published records of a mutillid parasitising bees of the genus *Leioproctus* (Taylor *et al.* 2019).

Acknowledgements

I am most grateful to Michael (Mick) J. Davis (formerly of the Western Australian Department of Environment and Conservation) for first alerting me to the presence of the nesting aggregation on Corackerup Creek and providing images and videos taken at the site. Access to the nesting site was facilitated by Dr Eddy Wajon who permitted me to stay on his property ‘Chingarrup Sanctuary’ on two occasions. I was assisted in my work at the site in January by Trevor Dempsey and Graham Zemunik, Graham taking and supplying the images of the nesting site that appear in this work. Peter Downes (Department of Earth and Planetary Sciences, Western Australian Museum) kindly confirmed the nesting medium as kaolinite. For his opinion on the identity of the bee forming the subject of this paper, I thank Remko Leijs (South Australian Museum). For identification of the gasteruptiid parasitoid, I thank John Jennings (University of Adelaide) and Ben Parslow (South Australian Museum). Christopher Taylor (University of Western Australia) kindly provided an opinion on the identity of the mutillid wasp.

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CONTRIBUTIONS TO THE NATURAL HISTORY OF *SCELIO FULGIDUS* CRAWFORD (HYMENOPTERA: PLATYGASTRIDAE)

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Abstract

Scelio fulgidus (Crawford, 1911) is a solitary hymenopteran egg parasitoid of the Australian plague locust (*Chortoicetes terminifera* (Walker, 1870)) and an important contributor to biotic population regulation in its primary host. The history of scientific research on the species is reviewed. Laboratory trials tested a number of aspects of *S. fulgidus* life history. Development duration from egg to adult was measured over a range of constant temperatures from 18–34°C. Complete development takes 4–6 days longer than *C. terminifera* embryonic development over the 24–34°C range, but diverges markedly below 24°C. Hatching takes over 300 days at 20°C and development is suspended at 18°C. Single females achieved complete parasitism of host pods in 80% of trials and females can parasitise 3 host pods in sequence. At 25°C, host egg pods were detected and parasitised up to 2 weeks after laying, therefore affecting all locust embryo stages up to and including anatrepsis, the rotation and inversion of the embryo position within the egg. Sibling mating produced male-biased sex ratios in offspring, outnumbering females after 2 generations.

Key Words: Australian plague locust, *Chortoicetes terminifera*, Acrididae

Introduction

The widely distributed platygastroid wasp genus *Scelio* Latreille, 1805 contains over 200 described species and all are obligate endoparasitoids of acridid eggs. The pest status of many locust and grasshopper species confers applied importance to research on *Scelio* biology and ecology, and some species have been investigated as potential biological control agents (Dangerfield *et al.* 2001, Greathead 1963).

Scelio fulgidus (Crawford, 1911) is a solitary egg parasitoid of the Australian plague locust (*Chortoicetes terminifera* (Walker, 1870)) and a significant parasite in terms of overall mortality in host populations. Instances of 90% parasitism of *C. terminifera* eggs in samples from dense host egg laying sites (egg beds) have been recorded (Farrow 1980, Deveson & Woodman 2014), but most populations are subject to much lower parasitism rates. Several *Scelio* species have been identified in *C. terminifera* eggs, but *S. fulgidus* accounts for almost all records, particularly in the semi-arid host range (Baker *et al.* 1996). *S. parvicornis* and *S. bipartitus* have occasionally been recorded, sometimes in association with *S. fulgidus*, and more often at the margins of the host range (Dangerfield *et al.* 2001, Baker & Piggott 1993).

S. fulgidus was first observed and described in *C. terminifera* in 1888 by naturalist farmer Richard Nancarrow near Bendigo, during a locust outbreak in Victoria. Richard Helms collected the species for the New South Wales (NSW) agriculture department in the Riverina in 1890. Government Entomologist Arthur Olliff sent the samples to Leland Howard, then assistant entomologist and Hymenoptera specialist with the USDA, who identified it as a species of *Scelio* (Deveson 2017).

S. fulgidus was named by American taxonomist James Crawford, from a cache of several species sent by NSW Government Entomologist Walter Froggatt (Crawford

1911). Crawford referred to Froggatt's note 'parasitic of *Pachystylus australis*' in NSW' (sample No. 60), which was the name he used for *Austroicetes cruciata* in 1900 (Froggatt 1900). Crawford named Froggatt's sample No. 96, collected from near Lake Cowal in 1901, *S. pulchellus*, now included in *S. chortoicetes*. Froggatt (1910) named *S. chortoicetes*, which is parasitic on *A. cruciata* and *A. vulgaris*, from the same Lake Cowal samples, suggesting confusion over sample labels or the taxonomic name of the host at the time. The species *S. fulgidus* was consolidated in the revision of the genus by Queensland entomologist Alan Dodd (1927).

Adult *Scelio* are <4 mm long, similar in size to the locust egg, reflecting their life history as endoparasitoids (Fig. 1). These minute wasp parasites came to public attention during locust outbreaks in the 1920's and 1930's. NSW entomologist Norman Noble conducted the first field and laboratory investigations of *S. fulgidus* ecology. He recorded locust and wasp hatching dates from egg beds near Moree in early summer 1934. Wasp emergence commenced around the same time as locust nymph hatchings, but continued for two months (Noble 1935). Noble (1938) also conducted microscopic examinations, recording a mean 233 ovarioles in each adult female and identifying the duration of larval and pupal stages within the host egg (Fig. 2).

During the 1955 locust plague, Victorian government entomologist Tom Hogan organised the collection of locust eggs from across Victoria and southern NSW to examine rates of *Scelio* parasitism. The proportion of *S. fulgidus* parasitism was highly variable between locations, ranging from 0–41% with a median of 5% (Hogan 1965).



Fig. 1. Adult female *Scelio fulgidus* (photo: James Woodman, APLC).

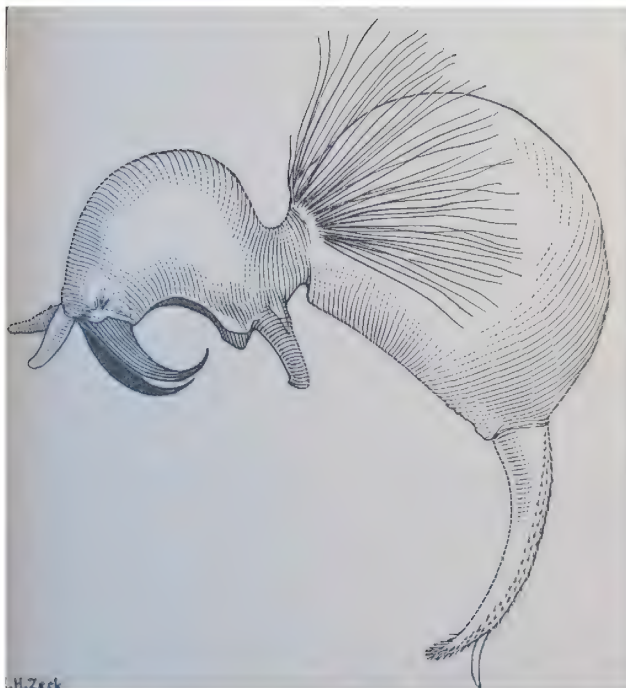


Fig. 2. First stage larva (greatly enlarged, actual size 0.2 mm) of *Scelio fulgidus*, from N.S. Noble (1935), *Agricultural Gazette of NSW*, p. 515 (drawn by E.H. Zeck).

CSIRO research led by Douglas Clark during the 1960s monitored rates of *S. fulgidus* parasitism in locust populations in Central West NSW. Clark (1972) recorded an increase in average egg parasitism rate from 9.8% (range 0–44%) in autumn 1969 to 35.5% (range 10–55%) the following summer. In the early 1970s, Roger Farrow also recorded a variable parasitism rate between sampled egg beds in the same region, with a local peak ~90% and a resultant host population collapse occurred in November 1973 near Trangie. This represented a 20-fold increase in parasitism over the previous autumn (Farrow 1980).

Noble (1935) reported anecdotal evidence that suggested *S. fulgidus* are carried on the wind with migrating locust swarms. Farrow (1981) identified *S. fulgidus* during net collecting of night-flying insects, indicating that this was a likely means of concomitant dispersal with host populations.

Graeme Baker and Ray Pigott of NSW Department of Agriculture conducted systematic sampling for *Scelio* parasites of *C. terminifera* during the 1990s (Baker *et al.* 1996). They reported a 0–79% range of parasitism of egg beds, with a mean of 19.8%. Baker & Piggott (1993) also identified *S. parvicornis* in a higher

proportion of egg pods than *S. fulgidus* during a locust outbreak on the NSW Northern Tablelands in 1981. David Hunter summarised numerous observations of *S. fulgidus* parasitism sampled from *C. terminifera* swarm egg beds during 1981–1991, reporting a wide variation in parasitism rate, with a mean maximum parasitism of 60% of egg pods during summer (Hunter *et al.* 1997).

The pattern of occurrence indicated by field data is of a variable rate of parasitism between egg beds and seasons, even at close separation distances, with highest rates in eggs laid during summer. Regional parasite abundance can increase in gregarious host populations that persist over several generations, indicative of lagged density dependence. The role of *S. fulgidus* in suppressing locust population increase has been discussed by various workers (Noble 1938, Clark 1972, Farrow 1982a, b). Farrow concluded that highest relative abundance often occurred as host populations declined, largely as a result of emigration, in an apparent inverse density-dependent relationship. However, all field estimates of parasitism rates come from high-density host egg bed sites and interactions at lower host densities are unknown.

This laboratory study addressed several aspects of *S. fulgidus* life history which remain poorly documented.

- Development rate of larval and pupal stages relative to the host over a range of temperatures
- The capacity of *S. fulgidus* females to successfully parasitise multiple egg pods
- Parasitism rate for single female oviposition in host pods
- The vulnerable host embryonic stages and post-laying duration of parasitoid detection
- Outcomes of sibling mating over several generations

Materials and Methods

a) Population sources

C. terminifera were obtained from a small colony maintained at Adelaide University during 2016–17. Small batches of locusts were freighted (2–4 days) in cardboard boxes over several laboratory generations and eggs laid by females were used in parasitism trials.

S. fulgidus were obtained from diapause host eggs collected from several egg-beds in the Coonamble–Coonabarabran area of Central West NSW in July 2015 and hatched in spring 2015. Trial insects came from 5 laboratory-reared generations in locust eggs.

b) Insect husbandry

Locusts were transferred to 30x30x30 cm mesh cages, incubated at 34°C 13:10 L:D and fed freshly cut seedling wheat daily. Egg pods were obtained by placing

single gravid females into small cardboard cups (237 mm) with 300 gm of packed soil at 8% water by weight. (Soil type red-brown chromosol; 35.2% coarse sand, 43.6% fine sand, 5.1% silt and 16.1% clay, pH 5.4). Cups were covered with fibreglass fly-screen mesh and placed under incandescent lamps during oviposition (32–37°C). After oviposition, soil cups were covered with Parafilm (Bemis Flexible Packaging, USA) and kept at $25 \pm 1^\circ\text{C}$ until used for parasitism trials.

After emerging from host egg pods, male and female wasps were placed together in plastic disposable food containers with perforated lids (15x10x7 cm, 20–30 in each) and incubated at 20.5°C on a 13:11 hour L:D photoperiod. 2 cm discs of paper towel, wet with weak sucrose solution, were placed in each container and re-wet with tap-water every 48 h to maximise wasp lifespan (Deveson & Woodman 2013). Female wasps were placed in uncovered soil cups containing host egg pods for parasitism tests. Offspring were treated as above and used in subsequent trials.

c) Parasitism trials

The standard assay used 1–3 adult female *S. fulgidus* of known age, placed at random in an oviposited soil cup under bench fluorescent lighting at 25°C . Wasps were observed for 10 minutes to allow time for exploration of the soil surface and detection of the host egg pod. Wasps often spent time entering soil crevices before encountering the oviposition chamber entrance. Most wasps spent 10–20 seconds inspecting the oviposition entrance with antennae before entering. In pods <5 days old, wasps chewed through the froth plug at the top of the oviposition hole. The majority of wasps entering the egg-pod chamber did not emerge again after a further 10 minutes, indicating parasitism could be occurring. Parasitising wasps usually remained in the egg chamber for >1 hour. Wasps entered irrespective of others already in the egg chamber and some used the entry hole chewed through the froth plug by the first wasp to enter the egg pod. Wasps that entered and then exited the host oviposition hole within 5 minutes were assumed not to have parasitised host eggs and were allowed to re-enter or were replaced. Wasps that flew or crawled out of the cup were returned up to 3 times. Those females that failed to enter the oviposition hole after 10 minutes were replaced by new females to ensure that each egg pod was potentially parasitised.

When the selected number of female wasps remained inside the egg pod chamber for at least 10 minutes, the cup was covered with parafilm and incubated for 24 h at $25 \pm 1^\circ\text{C}$ before transfer to final incubation temperature. This provided uniform initial conditions across the different temperature treatments, allowing time for *S. fulgidus* eggs to hatch before the final incubation temperature, thus avoiding any effect that very high or very low temperatures could have on parasitoid egg hatching.

For the time-delay trials that used host egg pods laid >5 days (up to 16 days) prior to *Scelio* introduction, the remains of any dried host froth caps were removed prior to wasp placement. This established uniformity across trials, because some

caps were dislodged or covered by soil during soil wetting. One pod was reserved from each treatment to allow for sampling during incubation to assess *Scelio* and host development stages.

Emergence of locusts and *Scelio* were recorded daily and the unhatched remainder of pods were examined for egg fate.

d) Examining unhatched remains and control egg pods

Egg pod remains were excavated and cleared from surrounding soil matrix 7–10 days after emergence ceased. Hatched but unemerged locust nymphs or *S. fulgidus* adults were recorded as hatched insects. Remaining host eggs were placed in a weak sodium hypochlorite solution for 10–20 minutes and then examined under a dissecting microscope. The number of first and second instar larvae, pupae or pharate adult *S. fulgidus* were recorded. Host embryo stage was identified following Wardhaugh (1978). Dead, withered or failed eggs (either no embryo, deteriorating or malformed embryo or congealed yolk) were identified and counted.

Visual detection of first instar larvae is not always possible in parasitised eggs because of their very small 0.1–0.3 mm size and hardening of parasitised host yolk in water. Potentially parasitized eggs were identified by the absence of a host embryo and yolk consistency. Parasitised eggs have a distinct liquid consistency, which spreads out on contact with water and congeals to a smooth white albumen within 5 minutes. Unparasitised locust egg yolk is granular and pale yellow. Subsamples of eggs with no visible locust embryo were opened and examined under a dissecting microscope to identify *S. fulgidus* larvae. On confirmation of first instar larvae in more than one subsampled egg, remaining eggs in the same state (no host embryo, clear yolk) were assigned as parasitised. Multiple larvae were detected in some treatments where several females had entered egg pods. Pods from which only locusts emerged and no *Scelio* larvae were identified in unhatched eggs were assumed to be unparasitised and were excluded from analyses (n=5 over all treatments).

e) Specific treatments

- To investigate development duration at different temperatures, multiple host pods parasitised by 1–3 female wasps were incubated at 34, 32, 30, 28, 26, 24, 22, 20 and 18°C constant temperatures in refrigerated incubators, with a 12:12 L:D photoperiod (Thermoline TRIL 495-1SD, temperature control accuracy $\pm 0.5^\circ\text{C}$). Emerging *S. fulgidus* and locust nymphs were recorded daily.
- To assess female relative parasitic performance, wasp and locust hatching numbers from host pods parasitised by single females used in the temperature and time delay trials <7 days were compared. Female capacity to parasitise multiple egg pods was tested by placing females of known age in separate oviposited cups at $25 \pm 1^\circ\text{C}$ to locate and parasitise the host egg pod. Cups were covered with parafilm. On the following day, emerged wasps were

transferred to new oviposited cups and this was repeated on a third day.

- Time to hatching of *S. fulgidus* eggs was examined at 25°C. 5 host egg pods of known age were parasitised by 2–5 female wasps to maximise the probability of first instar detection. Subsamples of 10 eggs were extracted after 12, 24, 48 and 168 hours and the numbers of identified first instar *S. fulgidus* were recorded.
- The possible diapause effect of photoperiod experienced by adults on subsequent larval development was tested at two photoperiods. On emergence, adult *S. fulgidus* were incubated in either 13:11 or 10:14 (L:D) photoperiod for 7 days. Females from each photoperiod were used to parasitise host pods at 1, 2, 3, 4 and 5 days after host laying and incubated at 30°C, and 1, 2, 3 and 4 days at 18°C, with 12:12 L:D. Paired host egg pods parasitised by wasps from each photoperiod for each time lag were compared for hatching times.
- Adult females of different known ages after emergence were tested for pod entry and parasitic behaviour (<12 hours–15 days) and to assess age in relation to parasitism rate.
- To test the ability of wasps to detect and parasitise host pods in wet or dry soil, oviposited soil cups were allowed to dry at 25±1°C for 5 days (but kept at 3% moisture by volume). *Scelio* females were placed in either dry or rewet soil cups (8% water by weight for 4 hours). Soil cups that were dry on wasp introduction were rewet after 30 minutes and all cups then covered with parafilm and incubated at 30°C (n = 6). Parasitism rate in wet and dry pods were compared.
- The ability of female wasps to detect and parasitise locust eggs relative to the time since the eggs were laid was tested over a range of delays after host oviposition and therefore at different host embryo stages. Soil cups with host egg pods were maintained at 25°C and 8% soil moisture for 0, 1, 2, 3, 4, 5, 6, 7, 9, 11, 12, 13 and 14 days after laying. A small number of diapause host eggs (stage 4C) were also obtained by transferring locusts to a 10:13 L: D photoperiod. Egg pod cups were covered with parafilm and kept at 25°C with soil moisture maintained prior to the introduction of wasps. 1–3 female *S. fulgidus* were introduced by standard assay and observed until parasitism was indicated. Soil cups were then covered with parafilm and incubated at either 25 or 30°C. Host embryonic development stage at each time delay was established by examining subsamples from control pods under a dissecting microscope. Embryo stage was assigned following the protocol of Wardhaugh (1978). Wasps were introduced to host pods at each embryonic development stage up to anatrepsis (stage 5).
- For the laboratory tests of sibling matings, females and males emerged from the same pod parasitised by a single female were kept together in plastic containers for 3–7 days. Single females were then placed in oviposited soil

cups <48 hours after host laying, following the standard assay. Soil cups were then incubated at 30, 32 or 34°C. Wasps emerging from this trial were reared in the same manner, producing a second generation of sibling-mated offspring. Subsequent trials were conducted on time-delayed host egg pods and not restricted to single female entry.

Results

S. fulgidus development duration at different temperatures

Development duration of *S. fulgidus* from oviposition to emergence was inversely proportional to temperature in the range 34–22°C, increasing from a mean of 19 days at 34°C to 54 days at 22°C (including the initial 24 hours at 25°C) (Table 1). There was a clear modal peak at each temperature >20°C (Fig. 3). The hatching period was <10 days at 26–34°C, but increased at lower temperatures, with emergence extending over 43 days at 24°C and >100 days at 22°C. Complete development of *S. fulgidus* takes 6 days longer than host embryonic development at 30–34°C range, and 4–5 days longer at 24–28°C (Fig. 4). Development duration relative to the host diverges at temperatures <24°C, taking >300 days at 20°C (200 days more than host embryos) and development is apparently suspended at 18°C.

For the 20°C trials, an increase of temperature to 30°C after the initial hatchings produced further hatchings in parasitised pods. At 18°C larvae remained at first instar after 245 days. Samples showed viable and sometimes multiple first instar larvae in eggs (see Fig. 6). Temperature was increased to 30°C and subsequent hatching recorded. The mean number of *Scelio* emerging from each pod in the 18°C trials was 29.2 (n = 8), similar to overall the mean at 22–28°C (27.5). The mode hatching day after temperature was increased was day 21 (n=86, from 234 total), 2 days later than the mode hatching day for direct incubation at 30°C.

Subsamples of 5–7 eggs were taken at intervals from control pods in temperature treatments at 20–28°C to record *Scelio* development stages. Preliminary information on transition through larval and pupal stages was recorded (Table 1). However, the number of days to the first observation of different larval stages can only be taken as maxima, because daily sampling was not undertaken due to the limitation of a single control pod at each temperature.

Eight visually distinguishable stages were identified in parasitised eggs (Appendix 1).

Multiple immature stages were identified in some samples. In the 24–28°C temperature range, the first instar lasts 10–15 days, rising to >30 days at 22°C. The second instar stage appears after about 10 days at 24–28°C and has the shortest duration, taking less than a week. Second instar larvae were not detected until after day 30 at 22°C. The first pupal stage was detected on day 16 at 28°C, and at day 20 at 24–26°C. Pupal stages lasted 10 days at 26–28°C and 20 days at 24°C. At 22°C, the spread of development stages increases, with first and second instar larvae, as well as pupae in samples from days 37 and 45.

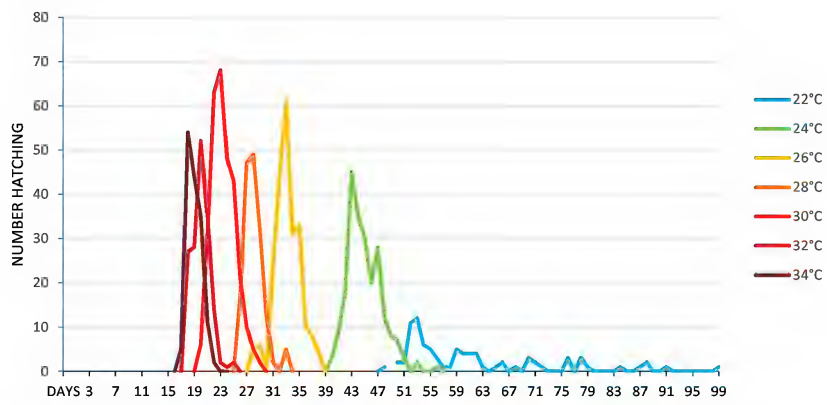


Fig. 3. Frequency of *Scelio fulgidus* hatching on each day after laying at different constant incubation temperatures. (Numbers for 30°C were divided by 3 to be equivalent to other temperatures).

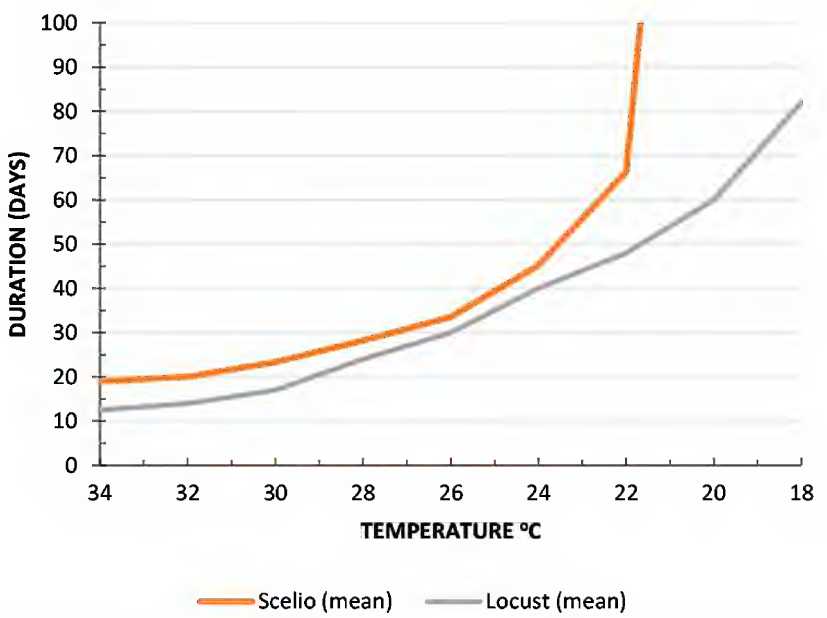


Fig. 4. Mean development duration of *Scelio fulgidus* and *Chortoicetes terminifera* from egg laying to hatch over a range of constant temperatures.

Female capacity to parasitise multiple egg pods and single female parasitism rate

In the trial of female parasitism of multiple host egg pods, wasp and locust hatchings were recorded for two wasps. One died after parasitising a second pod (trial 2). A single female (9 days old) successfully parasitised three host pods, producing 95 emerged male wasps, but died 48h after exiting the third pod (Table 2).

A larger sample would be necessary to establish the likely population distribution of fertility, or if some individuals survive to parasitise more than three host pods to achieve the potential fecundity >200 identified by Noble (1935).

From 16 host egg pods parasitised by a single female in other trials, the relative parasitism rate was estimated by comparing numbers of hatched wasps to locust nymphs. 13 parasitised pods showed complete parasitism (i.e. no locust emergence). Of the three pods where locust nymphs hatched, the wasp to locust ratio was 4.5: 1 (82: 18).

Effect of adult photoperiod on subsequent larval development

No clear difference was identified in development duration of offspring incubated at 30 or 18°C from adults reared under 13:11 or 10:14 (L:D) photoperiods. The small sample size (10 at 30°C, 8 at 18°C) limited further analysis of any refractory development expected to result from diapause (Diniz *et al.* 2017). However, any temperature-induced diapause at 18°C would likely have terminated and been undetectable after the long period of chilling.

Table 1. Development duration in days of *Scelio fulgidus* from laying to emergence at different constant temperatures. First sampled detection of immature life stages shown for 20–28°C.

Temperature °C	Number of host pods	Mean hatch day	Mode hatch day	Hatching range (days)	Second instar larvae	Early pupae	Final pupal stage
34	5	18.99	18	17–22	-	-	-
32	5	20.01	20	18–25	-	-	-
30	20	23.37	23	21–28	-	-	-
28	7	28.25	28	25–35	12	16	26
26	6	33.26	33	28–38	16	20	26
24	6	45.17	43	40–56	16	21	37
22	6	66.35	53	48–156	37	37	45
20	7	-	308	-	>150	>200	-
18	8	-	-	-	>250	-	-

Table 2. Parasitism by single female *Scelio fulgidus* over multiple host pods.

Trial	<i>Scelio</i> age	host pod ages	Pod 1 hatch		Pod 2 hatch		Pod 3 hatch	
			wasp	locust	wasp	locust	wasp	locust
1	9	5–7	46	0	35	1	14	11
2	<7	2–3	29	0	38	4	-	-

Age of females in relation to parasitism success

Newly hatched *S. fulgidus* were far less likely to remain in the soil cups, and spent less time investigating soil crevices or entering host pods, than those >24 h old. 3 newly emerged female wasps (<12 hours) were placed in each of 5 soil cups with 24-hour old host pods. Wasps were observed over 30 minutes. Young female wasps crawled out of cups and took flight frequently and were returned. 3 pods were entered, but wasps emerged within 5 minutes and did not re-enter, indicating that parasitism had not occurred. After 24 hours, the same wasps entered 4 of the host pods and had not re-emerged after 30 minutes, indicating parasitism was occurring.

Females at ages from 1–16 days parasitised host eggs. Trials with wasps 12–16 days old indicated a lower parasitism success on stage 3A embryos than with younger wasps. However, the sample size was too small to examine a possible fall in parasitism rate for older females (Table 4).

Time to hatching of *S. fulgidus* eggs

At 25°C, no first instar nymphs were identified in sampled eggs 12h after wasp oviposition. From the 10-egg subsamples at 24, 48 and 168h, 5, 10 and 9 first instar larvae were identified respectively.

Ability to detect and parasitise pods in wet or dry soil

Females successfully parasitised 5-day old host pods in wet and dry soil. No significant difference in parasitism behaviour or success was detectable between host pods in wet or dry soil due to the limited number of replicates.

Ability to detect and parasitise host pods relative to time since laying

S. fulgidus parasitised host eggs kept at 25°C for up to 16 days, affecting all host embryonic stages up to and including anatrepsis (Stage 5 of Wardhaugh 1978) (Table 3). At early host embryo stages (1–2), parasitism was either complete (no locust hatching) or very few locusts emerged. *Scelio* hatch as a proportion of total eggs was >80% in all except one trial. At host stages 3, 4 and 5, the proportion fell to <50%. However, relative parasitism (wasp: locust hatch) remained positive, with hatched wasps outnumbering locusts in all trials, except where wasps were >10 days old.

It is possible that parasitism could cause host mortality but not necessarily result

in *Scelio* completing development to hatching, particularly at later host embryonic stages. Unhatched eggs in each pod were therefore examined for any parasite or host development. Those that could be assigned to a development stage were recorded to indicate the cause of failure to hatch. Low numbers of failed *Scelio* larvae or pupae were identified in host egg stages 4A, 4B and diapause 4C, indicating host embryo mortality due to unsuccessful parasitism.

Trials on host stages 3–5 were conducted in August 2017, using wasps from a second generation of sibling breeding and the final batch of locusts from the Adelaide colony that subsequently died out (Jerome Buhl pers. com). Hatching results from an unparasitised control set (n=4) showed only 43% of eggs developed to hatching and average locust egg pod size was 27.5 eggs. Therefore, declining fertility of either *S. fulgidus* or the host could also have influenced these results.

Table 3. *Scelio* and locust hatch numbers after different delays from host laying to parasite introduction. Host embryo stages assessed from subsamples. Percentage *Scelio* hatch is relative to total host eggs, including failed eggs (unparasitized pods excluded). * indicates females <7 days old from sibling mating, († -temperature adjusted to produce specific embryo stage).

Host pod numbers	Days delay at 25° C	Incubation (°C)	<i>Scelio</i> age (days)	Locust embryo stage	Total eggs	<i>Scelio</i> hatch (% of total eggs)	Locust hatch
4	1	30	<7	1		167	1
2	2	25	<7	1	80	77 (91)	3
5	2	30	<7	1	138	131 (95)	0
8	3	25	*	1	243	141 (58)	25
4	3	30	<7	1	112	100 (89.3)	0
4	4	30	12	2	165	152 (92.1)	0
5	5	30	2–12	2	306	283 (92.4)	4
2	6	25	<7	2	87	81 (93.1)	1
3	7	25	<7	2	96	77 (80.2)	3
2	9	25	10–12	3A	80	14 (17.5)	45
4	11	24	*	3B	156	57 (36.5)	1
3	12	30	12–16	3B	109	34 (31.2)	60
5	12†	24	*	3C	115	34 (29.5)	11
6	13	25	*	4A	172	76 (44.2)	16
5	14	25	*	4B	169	22 (13.0)	5
3	18–21	25	*	4C diap	96	9 (9.4)	13
5	16	25	*	5	143	55 (38.5)	16



Fig. 5. *Scelio fulgidus* adults: (left) female; (right) male.

Separation of sexes and sex ratios

In gross morphology, *S. fulgidus* males are distinguished by the 10-segmented antennae that do not display the ‘U-shape’ curve of females (Figs. 1, 5). Males have a tyloid on the fifth antennal segment. The ovipositor may be visible on females that have laid eggs.

Examination of a large number of specimens ($n > 500$) showed that wing pigmentation is a more easily identified characteristic morphological difference. The distal half of female wings have a smoky pigment while male wings are clear (see Fig. 5).

The majority of host pods parasitised by a single female *S. fulgidus* produced mixed sex offspring (10 pods from a total of 19). Five pods produced exclusively male hatchings, presumably laid by unmated females, and 5 pods produced exclusively female clutches. The mixed-sex clutches were majority female, but included a small proportion of males. The female: male sex ratio in these mixed sex pods was 11: 1 (399: 36), whereas the overall sex ratio for temperature and photoperiod trials that included multiple females in host pods was 4.9: 1, largely as a result of the number of all-male pods.

Haplodiploidy and sibling mating

Dangerfield *et al.* (2001) stated that the occurrence of sibling mating was unknown in *Scelio*, despite being common among gregarious parasitoids. These trials were designed as a preliminary test of whether sibling mating occurs in co-confined *S. fulgidus* and of the parasitic success and sex ratios of offspring. Sibling mating was continued over two generations.

Results from these trials show that sibling mating produces viable offspring over multiple generations and overall parasitism rate is maintained. However, the M: F sex ratio of offspring from sibling-mated wasps at early host stages (1–2) was higher than in the mixed initial population, probably as a result of an increase in unmated females producing all male offspring. The female: male ratio in the initial mixed population trials was 4.9: 1, declining in first generation sibling-mated offspring to 4.2:1. The trend to male bias was more pronounced in subsequent sibling-mated generations, however later host embryo stages were used in these trials, so several possible causes could be involved.

Discussion

These experiments were designed as exploratory tests of some poorly documented aspects of the life history of a significant natural enemy of the Australian plague



Fig. 6. Separated first instar *S. fulgidus* larvae from host egg incubated at 18°C for 150 days (iPhone photo: Clare Mulcahy, APLC).

locust. Some trials necessarily involved small numbers and were run sequentially, combining effects such as host embryo stage and parasite sibling-mated status. Nevertheless, these limited data establish and extend biological knowledge about the potential for parasitism by individual wasps and for parasitism across host embryonic stages: information that is very relevant to the host-parasite ecology and provides the basis for further research.

These are the first data on development rate over a range of ecologically relevant temperatures and are sufficient to enable modelling of parasite development along with that of the host. The long development duration at temperatures <22°C alone could produce observed delays in the emergence of *S. fulgidus* relative to locust nymphs during spring. Soil temperatures during winter and spring could produce a continuity of adult wasps with the maturation of the spring locust generation. The much closer development time between parasitoid and host at higher temperatures (24–34°C) and shorter wasp longevity at higher temperatures may match host turnover during summer.

Noble (1938) observed parasitism of host egg pods after being covered for up to 48 hours. Clark (1972) reported that experiments indicated *S. fulgidus* was able to parasitise host eggs up to three weeks after pods were laid. Those results were not published and it is not known if they came from field or laboratory observations. These trials show *S. fulgidus* can detect, successfully parasitise and cause host embryo mortality at least until anatrepsis stage, approximately half of the total embryonic development. A limit to host embryo susceptibility stage was not found because older embryo stages were not tested. These results suggest a lower parasitism success rate but continued host mortality at locust embryo stages 3–5. There is therefore potential for wasps hatching in autumn to parasitise diapause host eggs several weeks after host oviposition. Further research could clarify the susceptible host embryo stages or if mortality occurs beyond host embryo anatrepsis at stage 5.

Table 4. Sex ratios of offspring from sibling-mated *Scelio fulgidus* trials. Number of host pods, embryo stage and sibling-mated wasp generation number shown for each trial. Numbers of female, male and mixed-sex wasp egg clutches, total hatchings by sex and ratios shown.

Total pods	Host stage	<i>Scelio</i> generation	Female clutch	Male clutch	Mixed clutch	Total ♀	Total ♂	♀ : ♂ ratio
15	1	1	2	2	11	338	81	4.2 : 1
14	1	2	0	6	8	131	101	1.3 : 1
12	2	2	1	5	6	153	76	2.0 : 1
8	3	2	0	1	7	34	52	1 : 1.5
9	4	3	0	1	3	44	58	1 : 1.3
5	5	3	0	5	0	-	49	0 : 1.0

Noble (1938) gave an incubation period of 24h for *S. fulgidus* samples from the field, but the temperature was not specified. This is supported by examination of host eggs at 25°C. First instar larvae were detected in the majority of eggs 24 and 48h after parasitism. Noble (1938) examined field-laid host eggs in the laboratory and recorded the appearance of larval stages. These trials showed similar timing of development stages at 26°C.

Superparasitism by *S. fulgidus* is common in the field, with up to 8 first instar larvae reported in host eggs (Noble 1938). This is the result of several females ovipositing in the same host egg rather than self-super parasitism or ‘siblicide’. *Scelio* are solitary endoparasitoids, and larvae eliminate competitors both by combat and interference competition. The latter could involve allelochemical toxins against conspecifics in the absence of direct physical encounter. Host eggs are grouped tightly in pods and females systematically oviposit in many eggs, but whether individual females keep track of which eggs have been parasitised by marking is unknown. The actions of wasps moving and ovipositing the tightly packed host eggs within a pod are not well documented. The possible effect of superparasitism on the later parasitic performance of survivor larvae (Devescovi *et al.* 2017) was not examined here.

The elimination of supernumerary larvae is a necessary consequence of the proximal constraint of limited resources that allow only a single individual to complete development. The heavily sclerotised mandibles and the motility of first instar larvae are involved in encounters or ‘combat’ to kill competitor larvae in other Hymenoptera endoparasitoids (Lawrence 1988, Fisher 1971). Host embryos are more likely to be killed by molecules or ‘toxins’ in venom delivered during *Scelio* adult oviposition, because the composition of host egg yolk is altered soon after oviposition when parasitic larvae are at first instar (Asgari & Rivers 2011). *Scelio* are solitary idiobiont parasitoids, meaning that infection causes host death and the number of larvae is reduced to one before transition to the second instar. Under superparasitism, mortality of all larvae could occur, so the number of emerging wasps may not reflect the actual parasitism rate.

Like all members of the Hymenoptera, *Scelio* species have a haplodiploid sex-determination breeding system. Males are haploid, with only one set of chromosomes; females are diploid and develop from fertilised eggs. Results here demonstrate that *Scelio* are arrhenotokous, a common mode of reproduction among parasitic wasps. Unmated females can lay only hemizygous haploid eggs and therefore produce male offspring, but mated females control the fertilisation of eggs at laying to produce both male and female offspring (Dangerfield *et al.* 2001, van Wildenburg *et al.* 2006). The small proportion of males (9%) from majority female clutches in host pods parasitised by single female wasps in these trials are from eggs selectively left unfertilised.

Sibling mating is possible at pre- or early post-emergence from the host oviposition site and the close genetic relationship between such siblings introduces the potential for inbreeding. However, the consequences may not be evolutionarily

negative and behavioural ecology can reduce its incidence (Penaccio & Strand 2006). The results of sibling mating over two generations here show a trend to male-biased sex ratios, outnumbering females after two generations. This results from an increase in pods laid by unmated females, possibly due to mating avoidance by females, or lower male fertility, although host embryo stage could also have influenced the results. The trials on older locust embryos and sibling-mated female wasps were combined here, which reduces the ability to draw inference from either. The trend toward greater male bias in inbreeding trials has been used as an indicator of single-locus allelic sex determination systems (van Wildenburg *et al.* 2006). The results suggest this form of sex-determination applies for *Scelio*, although genomic analyses would be necessary for verification.

Previous observations using clear plastic cups indicated that emergence of *S. fulgidus* from host eggs takes place in a sequential manner from the top eggs in the pod, so wasps do not engage in competition to reach the surface and the chance of sibling mating may be reduced. Superparasitism at high host densities and the greater propensity of newly emerged females for flight could also reduce the occurrence of sibling mating in the field. The early flight activity of *S. fulgidus* could also be related to a post-teneral dispersal syndrome, adapted to the migratory behaviour of its host.

The work of Noble (1935) established a mean of 233 ovarioles in immature female wasps. *S. fulgidus* is therefore likely proovigenic, meaning females have the full lifetime fecundity complement of ovarioles on emergence from host eggs (Jervis *et al.* 2008). Limited examples here show individual females can successfully parasitise three host pods and some individuals could approach their fecundity potential when host egg pods are locally abundant. Evolutionary biologists have grouped particular traits of Hymenopteran parasitoids to identify unifying features and build hypotheses over ecological and evolutionary relationships between taxa. The occurrence of proovigeny among idiobionts, as occurs in *S. fulgidus*, is relatively rare and may be a particular trait of egg parasitoids (Jervis & Ferns 2008).

The question of whether *S. fulgidus* larvae enter diapause at first instar stage, as has been reported for this and other species, remains uncertain (Dangerfield *et al.* 2001). The long period of dormancy without increased mortality in larval *S. fulgidus* at 18–20°C suggests protective suppression of metabolic processes and this may be an example of temperature-induced diapause. Development of larvae from the 18°C treatment after the increase in temperature was not refractory as would be expected with diapause (Diniz *et al.* 2017), but reactivation occurred after a long period of chilling so diapause development could have been completed.

Rearing adults at long- or short-day photoperiods did not change the immature development duration of offspring in the small number of samples taken here. Baker & Pigott (1993) used evidence for a bimodal development duration to hatching in *S. parvicornis* sampled from *C. terminifera* egg pods in winter

as evidence of diapause in a small proportion of wasp larvae. They suggested that diapause coincided with exposure to soil temperatures below development threshold ($<15^{\circ}\text{C}$). Baker *et al.* (1985) and Hunter *et al.* (1998) reasoned that hatching of *S. fulgidus* from diapausing host eggs in autumn indicated a lower diapause-inducing temperature than that of the host.

For at least half of their development period, host embryos are susceptible to mortality from *S. fulgidus*, which could last for several weeks at temperatures experienced during spring and autumn. However, field observations indicate that wasp activity declines at locust egg beds within a few days of the cessation of host laying (Noble 1938). Detectability of host egg pods is likely to decline through time due to soil surface disturbance, but swarming locusts can continue to visit and lay in the same egg bed for a week or more, potentially exposing all host eggs to parasitism.

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Appendix 1.

- First instar larvae (minute, mobile, ~ 0.1–0.3 mm) (Fig. 6).
 - Second instars were separated into early and late, based upon the size of the globular larval form.
 - Late second instars are more elongate and occupy more than half the host egg.
 - Early and late stage pupae were distinguished by body form and pigmentation. The early stage is white and some appendages may not be clearly defined. The head faces the micropylar end of the egg.
 - Late stage pupae are characterised by dark pigmentation of the eyes, followed by parts of the pronotum and scutum.
 - The final pupal stage was defined by complete dark cuticle pigmentation, progressing to the legs and abdomen, but characteristically not extending along the lateral edges of the abdomen.
 - Pharate adults are fully formed with only a residual plug of white meconium at the distal end of the host egg and a narrow thread visible to the tip of the abdomen.
 - Adults remain in the empty host egg chorion, which takes on an orange colour, and are immediately active when the egg is opened.
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